

COMPARATIVE STUDY OF MOUTHPARTS OF PREDACEOUS MIDGES OF
THE TRIBE PALPOMYIINI (DIPTERA: CERATOPOGONIDAE) FROM
EASTERN UNITED STATES

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Abstract.—Mouthparts of females of 16 species and males of 13 species representing *Bezzia*, *Phaenobezzia*, and *Palpomyia* of the insectivorous tribe Palpomyiini were examined by light and scanning electron microscopy. Greatest differences among species occurred in the sclerotized mandibles of females where the mean number of coarse medial teeth ranged from 6.00 to 10.31, small basal teeth from 0.37 to 3.47, length of the tooth row in relation to length of the mandible from 14.9 to 29.8% and mean number of lateral teeth from 1.50 to 6.61. An interlocking mechanism midlength of the blade functions as a fulcrum; abduction of the base of the mandibles results in divergence of their tips and enables their strong teeth to cut the cuticle of the prey. The non-insectivorous males have mandibles with large medial non-functional teeth and lack an interlocking mechanism. Lateral teeth are present on the mandibles of some males of eight species.

The unarmored labrum, hypopharynx and lacinia are inserted into the wound made by the mandibles. The mandibles remain between the labrum and hypopharynx during feeding and serve as the floor of the food canal and roof of the salivary canal. The laciniae, which are smooth in both sexes, form the lateral proximal boundaries of the food canal. Cylindrical structures at the tip of the labrum of females are thought to be mechanoreceptors, chemoreceptors or both; they are reduced in size or absent in males and, in most species, are replaced by spicules. Labra of males and females have species specific characters, but differences are less pronounced in males. The hypopharynx of females is generically specific in its shape and species specific in distribution of its spicules. The hypopharynx of males is species specific in size and shape of its spicules which are longer than in those of conspecific females.

Sensilla on the maxillary palp sensory organ are species specific in both sexes with respect to number, points of origin on the palp of individual sensilla, shape of the head of the sensilla and total length. The number of sensilla per sensory organ is approximately equal in both sexes of a given species and they probably do not function in prey detection and/or location, which is thought to be more related to visual stimuli in predaceous midges.

Key Words: Insecta, Ceratopogonini, Palpomyiini, mouthparts

The Palpomyiini Enderlein, one of the insectivorous tribes of Ceratopogonidae Newman is comprised of the genera *Amerohelea* Grogan and Wirth, *Bezzia* Kieffer,

Clastrieromyia Spinelli and Grogan, *Pachyhelea* (Wirth), *Palpomyia* Meigen, and *Phaenobezzia* Haeselbarth (Spinelli and Grogan 1985). Females of this tribe, as well

as those of Heteromyiini Wirth, and Sphaeromyiini Newman, and most Ceratopogonini Newman feed on Chironomidae, Chaoboridae and Ephemeroptera (mayflies), usually males, that are captured from mating swarms. In addition, in Palpomyiini, Heteromyiini and Sphaeromyiini, when the female enters mating swarms of her own species, she captures a male that she feeds upon while he is in copula with her (Downes 1977). Females of the tribe Stenoxenini Coquillett also have well developed mandibles with large teeth, thus indicating that they too are insectivorous; however, observations on their swarming, mating or feeding habits are lacking (Wirth and Ratanaworabhan 1972).

Mouthparts of both males and females of an insectivorous species of Ceratopogonidae, *Probezzia* (as *Dicrobezzia*) *venusta* (Meigen), a member of the Sphaeromyiini were described in detail by Gad (1951). All structures were present in both sexes, with male structures being smaller and less developed. Gad also presented data and drawings of some structures of other insectivorous genera, including *Bezzia* and *Palpomyia*, and compared mouthparts of insectivorous forms with hematophagous and flower-feeding representatives of the family. Downes illustrated and briefly described mouthparts of *Probezzia flavovigra* Coquillett (1971) and *Palpomyia quadrispinosa* Goetgebuer (1978). Mouthparts of insectivorous Ceratopogoninae are characterized by large mandibular teeth and reduced, toothless laciniae, an exception being members of the insectivorous *anophelis* group of *Culicoides* Latreille subgenus *Trithecooides* Wirth and Hubert that have large mandibular teeth and toothed laciniae (Wirth and Hubert 1989). Hematophagous forms, e.g. *Culicoides* have small, closely set mandibular teeth and toothed laciniae. Gad found the tips of the mandibles, labrum, laciniae, and hypopharynx to be weakly sclerotized and without functional teeth in *Atrichopogon pavidus* (Winnertz), subfamily Forci-

pomyiinae; therefore, he considered the species to be a nectar feeder.

Many studies have used mouthpart structure to distinguish taxa. For example, Wirth and Hubert (1959) used the structures of elements of the proboscis of the subgenus *Trithecooides* (tribe Culicoidini), for identification of species and species groups. Glukhova (1982) found that each element of the proboscis of 13 species of *Trithecooides* exhibited considerable species diversity, in contrast to a high degree of similarity of other structures (wing, maxillary palpus and spermathecae), and used diversity of these elements as diagnostic characters. She found no species-specific differences in the maxillary palpus of species of *Trithecooides*, but Chaika (1978) found the palpal sensory organ to be of taxonomic significance in some other species of *Culicoides*. Endoparasitic species of *Atrichopogon* Kieff. (subfamily Forcipomyiinae), were divided into four groups by Glukhova (1981) based upon structure of the female mouthparts. She related this diversity to differences in the various insect hosts (beetles, lacewings, dragonflies, etc.) and the parts of their body upon which these ectoparasitic species feed. She found even greater diversity in mouthparts of species of the related genus *Forcipomyia* which she attributed to diversity of their hosts. Wirth and Grogan (1988) included mandibles and palpi to partially characterize genera of Ceratopogonini. In a recent comparative study of ten species representing seven genera of predaceous midges of the tribe Ceratopogonini, we found the mandibles, labrum and palpal sensory organs of females to be species specific and the hypopharynx generically specific (McKeever et al. 1991).

Descriptions of mouthparts of the predaceous midge tribe Palpomyiini (subfamily Ceratopogoninae) are few and generally confined to the mandibles. Dow and Turner (1976) presented data on the number of mandibular teeth of female *Bezzia* along with drawings of female mandibles of five of their 40 Nearctic species. Wirth (1983a)

presented data on the number of mandibular teeth of two species of *Bezzia* with a drawing of the mandible of one. In a later paper, Wirth (1983b) presented drawings, accompanied by data on the number of teeth, for mandibles of seven species of *Bezzia* females, as well as a drawing of the male mandible of one species. Wirth and Grogan (1983) gave data on the number of mandibular teeth of all species of *Bezzia*. Grogan and Wirth (1981) presented data on the number of mandibular teeth of 10 species of *Amerohelea* accompanied by drawings of the mandibles of two of the species; all of these species occur in Central and South America, and one is found in southwestern United States as well. Grogan and Wirth (1979) gave the number of mandibular teeth of female *Palpomyia* of North America and presented drawings of the mandibles of females of nine of thirty-one species and males of three species. Downes (1978) presented photomicrographs of mouthparts of female *Palpomyia quadrispinosa* Goetghebuer and discussed in detail their functions. Wirth and Grogan (1982) presented a drawing of the female mandible of *Phaenobezzia opaca* (Loew), and Gad (1951) illustrated the female mandible of *Palpomyia luteifemorata* Edwards. To date, no studies of mouthparts of predaceous Palpomyiini have employed electron microscopy. This is a report of a detailed comparative study, by light and scanning electron microscopy (SEM), of the morphology of mouthparts of females of 16 species and males of 13 species in three genera of Palpomyiini to determine whether generic differences or species-specific differences, or both, exist in any or all structures of the mouthparts.

MATERIALS AND METHODS

Females of the following species were examined: *Bezzia bivittata* (Coquillett), *B. imbibida* Dow and Turner, *B. nobilis* (Winertz), *B. glabra* (Coquillett), *B. dorsasetula* Dow and Turner, *Phaenobezzia opaca*, *Palpomyia subaspera* (Coquillett), *P. cressoni* (Malloch), *P. lineata* (Meigen), *P. ple-*

beia (Loew), *P. rufa* (Loew), *P. pseudorufa* Grogan and Wirth, *P. basalis* (Walker), *P. flaviceps* (Johannsen), *P. scalpellifera* Grogan and Wirth, and *P. hastata* Grogan and Wirth. Males of all the foregoing species except *P. cressoni*, *P. flaviceps* and *P. hastata* were examined.

All specimens except 13 *P. nobilis* that were collected at Hatchet Creek, Alachua County, Florida, were collected on Patuxent Wildlife Research Center and Beltsville Agricultural Research Station, both near Laurel, Prince Georges County, Maryland or at Salisbury, Wicomico County, Maryland. Specimens were collected with Malaise traps or by sweeping vegetation and stored in 70% ethanol. Later, they were dehydrated in a graded ethanol series, dried in a critical point drier and dissected with tungsten needles sharpened in boiling potassium nitrate. Dissected structures were suspended horizontally from fresh micro-drops of CMC mounting medium (Turtox, Chicago) on 15 mm glass coverslips that had previously been coated with a thin film of CMC. Specimens were examined with a light microscope, measured, then gold-coated and later photographed with an ISI Super II scanning electron microscope.

Measurements of 13 characters of the various mouthparts of 127 females and 77 males were made with an ocular micrometer at 400 \times and values expressed in micrometers (μm). In addition, the number of mandibular teeth was determined at 400 \times . The number of spicules on the labrum and hypopharynx and the number of palpal sensillae were counted directly on the SEM screen. Length of the sensilla and camber and pitch of the mandibular teeth were determined from SEM photomicrographs. Statistical differences were determined by *t*-tests. Measurements were determined as in our previous study (McKeever et al. 1991) as follows.

Mandibles: (total length)—from attachment of adductor muscle at outer angle of base of mandible to tip of distal tooth; (length of tooth row)—from proximal base

Table 1. Measurements (μm) of mandibles of female Palpomyiini.

Species	Total Length			Maximum Width			Width at Basal Tooth			Length of Tooth Row		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
<i>B. bivittata</i>	142.10	13.46	13	32.12	2.86	13	18.21	4.33	13	33.04	3.98	13
<i>B. imbifida</i>	170.00	6.56	11	31.70	1.68	12	9.84	2.73	12	40.12	3.36	12
<i>B. nobilis</i>	168.77	5.32	34	36.09	1.18	37	19.44	1.35	39	50.29	32.59	38
<i>B. glabra</i>	177.72	9.99	24	37.65	2.78	26	19.58	3.54	25	49.26	5.96	25
<i>B. dorsasetula</i>	126.34	6.36	33	27.26	0.74	35	12.94	0.49	33	29.88	1.21	32
<i>Ph. opaca</i>	147.06	5.48	37	34.20	1.45	35	14.29	0.73	39	27.03	1.50	37
<i>P. subaspera</i>	232.08	—	2	43.22	—	2	25.93	—	2	64.50	—	2
<i>P. cressoni</i>	186.58	3.07	7	45.88	2.62	10	15.56	1.27	10	38.04	3.62	10
<i>P. lineata</i>	206.83	15.67	8	43.74	3.56	9	18.62	3.54	9	55.27	8.52	9
<i>P. plebeia</i>	158.20	3.01	19	30.47	0.81	22	11.91	0.56	22	33.67	0.88	22
<i>P. rufa</i>	205.66	6.99	34	39.04	1.55	34	17.11	2.07	35	43.70	2.45	35
<i>P. pseudorufa</i>	159.41	3.48	28	28.60	0.94	29	10.92	1.11	28	37.00	1.90	8
<i>P. basalis</i>	152.95	8.10	4	35.24	3.67	4	14.30	3.16	4	28.26	20.30	4
<i>P. flaviceps</i>	149.99	5.27	22	32.22	1.41	24	14.26	1.12	25	30.08	1.83	26
<i>P. scalpellifera</i>	173.23	22.05	8	36.41	4.48	8	13.96	0.59	8	25.77	1.45	8
<i>P. hastata</i>	146.96	—	2	33.21	—	2	12.46	—	2	24.60	—	2

of proximal tooth to tip of distal tooth; (maximum width)—from medial to lateral edges, near midpoint, measured at 90° to long axis of mandible; (width of basal tooth)—from proximal base of proximal tooth to lateral edges, measured at 90° to long axis of mandible; (length of longest tooth)—from tip to base; (camber of the teeth)—proximal angle between distal edge of the fifth tooth (line from tip to distal base) and a line parallel to base of the tooth row; (pitch of teeth)—proximal angle between proximal edge of the fifth tooth (line from tip to proximal base) and a line parallel to base of the tooth row.

Labrum: (length)—from junction with hypopharynx to tip; (width)—maximum immediately proximal to teeth.

Hypopharynx: (length)—from junction with labrum to tip; (width)—maximum immediately proximal to teeth.

Laciniae: (length)—from junction with maxillary palpus to tip; (greatest width)—distance between lateral edges at junction with maxillary palpus, measured at 90° to long axis of the laciniae.

Sensilla: (length)—from origin in socket to apex.

There are no voucher specimens, because

the specimens were destroyed in preparing the mouthparts for examination. Specimens of all species described herein are in the Florida State Collection of Arthropods, Gainesville, the U.S. National Museum of Natural History, Washington, D.C., and the Canadian National Collection of Insects, Ottawa. The mandible, labrum, hypopharynx, lacinia, and palpal sensillae are illustrated by SEM photomicrographs (Figs. 1–17). Size relationships of the structures are presented tabularly, as the mean and two standard errors. (Tables 1–8).

RESULTS

General Descriptions of Structures

Mandible.—The strongly sclerotized mandibles of females have an interlocking mechanism approximately midlength of the blade that is similar in structure and function to that described for *Culicoides* (Gad 1951) and the Ceratopogonini (McKeever et al. 1991). On the medial edge the distal first and usually second antrorse teeth are followed by a series of longer, coarse, retrorse teeth that may be uniform throughout or may decrease in length and size proximally (Figs. 1–5). There were 6–17 such

Table 2. Measurements (μm) and number of teeth of mandibles of female Palpomyiini.

Species	Length of Longest Tooth			No. of Coarse Medial Teeth			No. of Small Basal Teeth			No. of Lateral Teeth		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
<i>B. bivittata</i>	3.17	0.41	13	10.31	1.52	19	3.47	1.40	19	3.20	1.00	20
<i>B. imbifida</i>	2.71	0.12	12	9.42	0.99	12	2.17	0.59	12	3.75	0.61	12
<i>B. nobilis</i>	4.41	0.27	39	8.96	0.25	45	3.35	0.59	45	4.44	0.47	45
<i>B. glabra</i>	5.19	0.44	26	10.11	1.12	27	1.78	0.55	27	5.00	0.89	27
<i>B. dorsasetula</i>	2.72	0.09	33	7.71	0.27	31	2.58	0.54	31	3.64	0.55	33
<i>Ph. opaca</i>	6.27	0.33	39	7.07	0.10	45	0.89	0.30	45	6.61	3.36	44
<i>P. subaspera</i>	7.98	—	2	9.50	—	2	2.00	—	2	3.50	—	2
<i>P. cressoni</i>	5.59	0.60	39	7.10	0.63	10	2.60	0.69	10	4.09	1.04	10
<i>P. lineata</i>	5.91	0.90	9	8.29	0.79	14	4.71	0.83	14	6.57	0.43	14
<i>P. plebeia</i>	5.56	0.35	22	7.05	0.17	21	2.86	0.50	21	4.54	0.45	22
<i>P. rufa</i>	5.69	0.28	34	7.10	0.15	41	3.27	0.47	41	3.78	0.58	41
<i>P. pseudorufa</i>	4.54	0.32	28	6.97	0.13	35	2.08	0.38	35	3.09	0.54	35
<i>P. basalis</i>	3.99	0.00	4	6.00	—	8	0.37	0.89	8	3.75	0.59	8
<i>P. flaviceps</i>	3.09	0.33	26	7.06	0.34	33	1.06	0.43	33	2.27	0.69	33
<i>P. scalpellifera</i>	4.40	0.66	8	6.25	0.43	8	1.87	0.94	8	5.29	1.38	7
<i>P. hastata</i>	2.66	—	2	6.00	—	2	1.50	—	2	1.50	—	2

teeth on the distal 14.9 to 29.8% of the blade in all 16 species examined. Proximally, up to eight small basal teeth may be present. Up to 11 small, antrorse projections, considered to be accessory teeth, may occur on the lateral edge in all species, but these may be absent in some specimens. Greatest width of the mandible ranges from 18–24% of the total length among the 16

species and is attained at the point of the interlocking mechanism; little or no decrease occurs proximally. The base curves approximately 45–90° to the long axis of the blade. Muscle attachment and function are as described for the Ceratopogonini (McKeever et al. 1991).

Mandibles of males of the 13 species examined are poorly sclerotized, broad blades

Table 3. Measurements (μm) and number of spicules of labra and hypopharynx of female Palpomyiini.

Species	Labra						Hypopharynx					
	Total Length			No. of Spicules			Total Length			No. of Spicules		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
<i>B. bivittata</i>	170.24	22.40	5	19.50	6.02	4	170.05	19.02	7	20.75	11.93	4
<i>B. imbifida</i>	177.23	5.38	3	25.20	4.51	5	178.78	1.91	3	19.33	1.84	6
<i>B. nobilis</i>	189.60	10.99	18	25.14	4.42	7	199.20	10.47	16	29.27	6.37	11
<i>B. glabra</i>	209.70	16.20	12	19.64	3.91	11	219.51	17.98	12	23.36	5.62	11
<i>B. dorsasetula</i>	158.36	3.54	15	17.92	1.68	12	155.14	4.33	17	20.50	1.46	14
<i>Ph. opaca</i>	188.73	16.66	14	26.12	1.69	17	185.40	15.66	15	15.94	5.53	17
<i>P. subaspera</i>	266.00	—	1	21.00	—	1	251.37	—	1	36.00	—	1
<i>P. cressoni</i>	223.08	35.64	3	18.00	7.45	3	217.68	39.98	3	37.91	10.24	5
<i>P. lineata</i>	249.25	30.24	3	20.50	—	2	268.55	—	1	24.00	—	1
<i>P. plebeia</i>	184.37	8.59	8	23.37	3.19	7	179.81	8.95	9	—	—	0
<i>P. rufa</i>	239.09	12.19	12	15.83	3.14	6	244.40	15.62	13	11.75	6.67	4
<i>P. pseudorufa</i>	187.29	8.06	11	17.22	2.87	9	187.33	7.07	12	19.62	4.66	8
<i>P. basalis</i>	183.54	—	2	—	—	0	186.20	—	2	7.00	—	2
<i>P. flaviceps</i>	169.29	11.98	7	18.57	7.04	7	167.36	8.46	12	5.60	5.38	5
<i>P. scalpellifera</i>	198.83	39.42	4	—	—	0	197.73	71.81	3	10.00	—	2
<i>P. hastata</i>	—	—	0	18.00	—	1	—	—	0	6.00	—	1

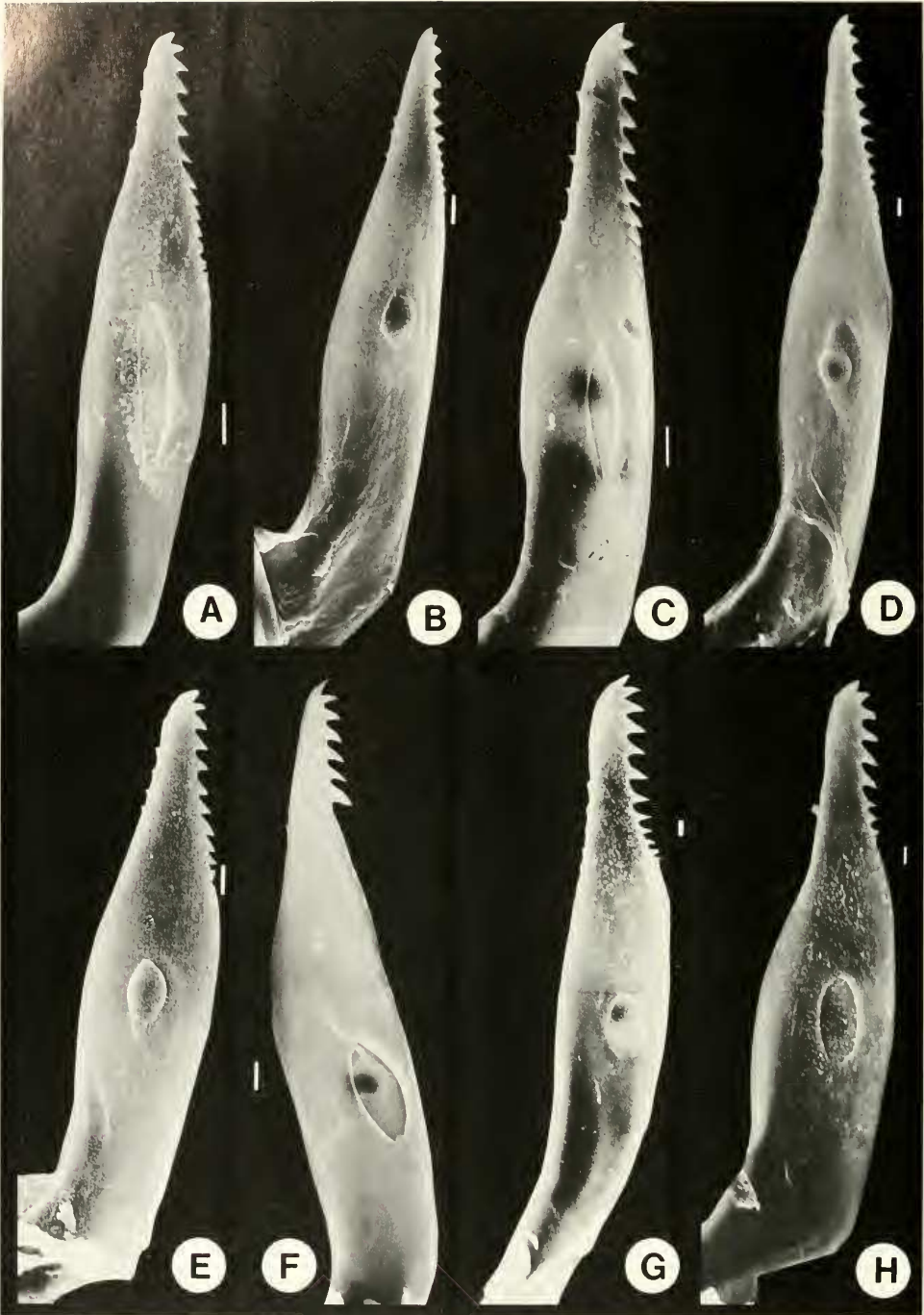


Fig. 1. SEM photomicrographs of mandibles of female. A, *Bezzia bivittata*. B, *B. iubifida*. C, *B. uobilis*. D, *B. glabra*. E, *B. dorsasetula*. F, *Phaenobezzia opaca*. G, *Palpomyia subaspera*. H, *P. cressoni*. White bars equal 8 μ m.

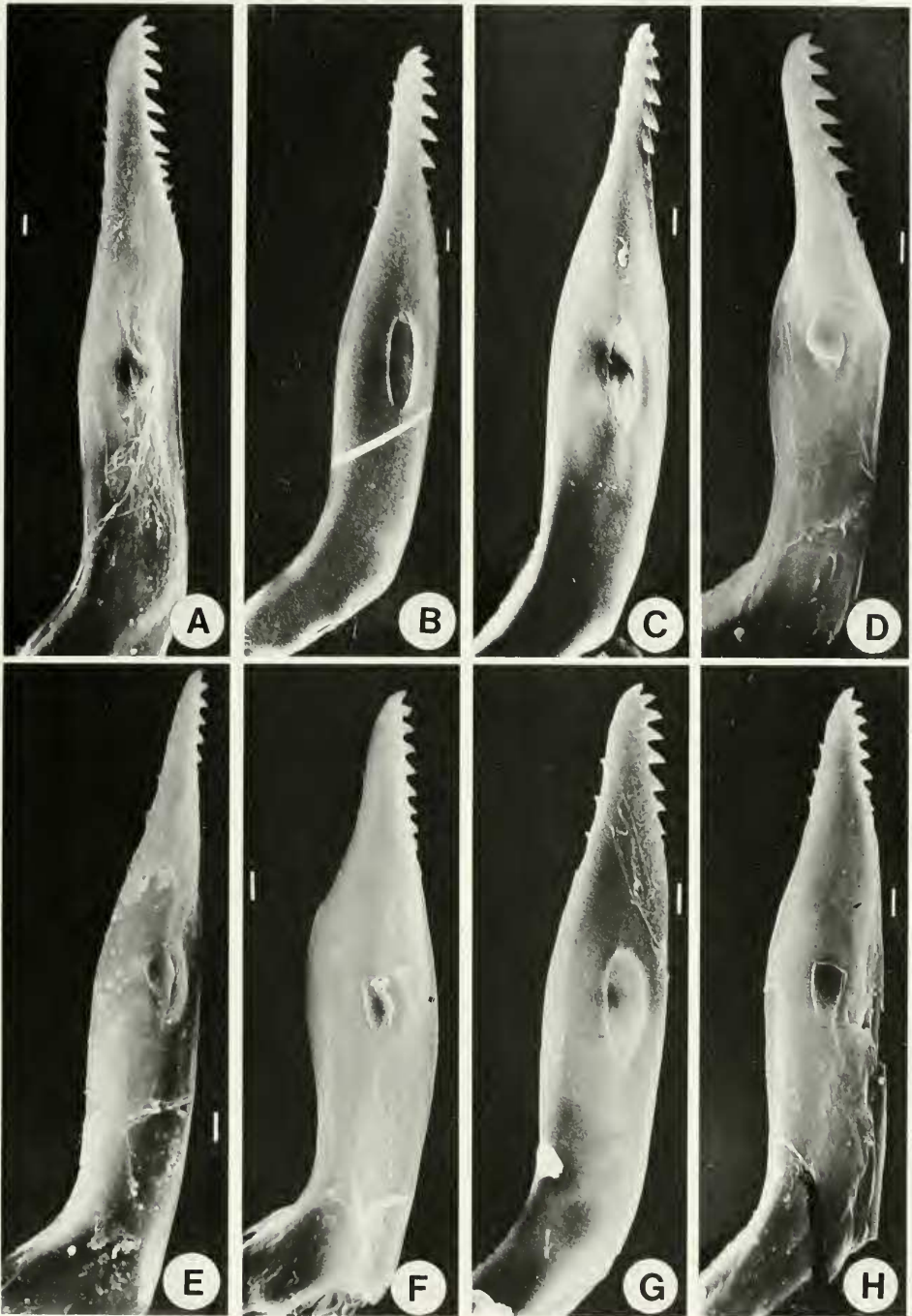


Fig. 2. SEM photomicrographs of mandibles of female. A, *Palpomyia lineata*. B, *P. plebeia*. C, *P. rufa*. D, *P. pseudorufa*. E, *P. basalis*. F, *P. flaviceps*. G, *P. scalpellifera*. H, *P. hastata*. White bars equal 8 μm .

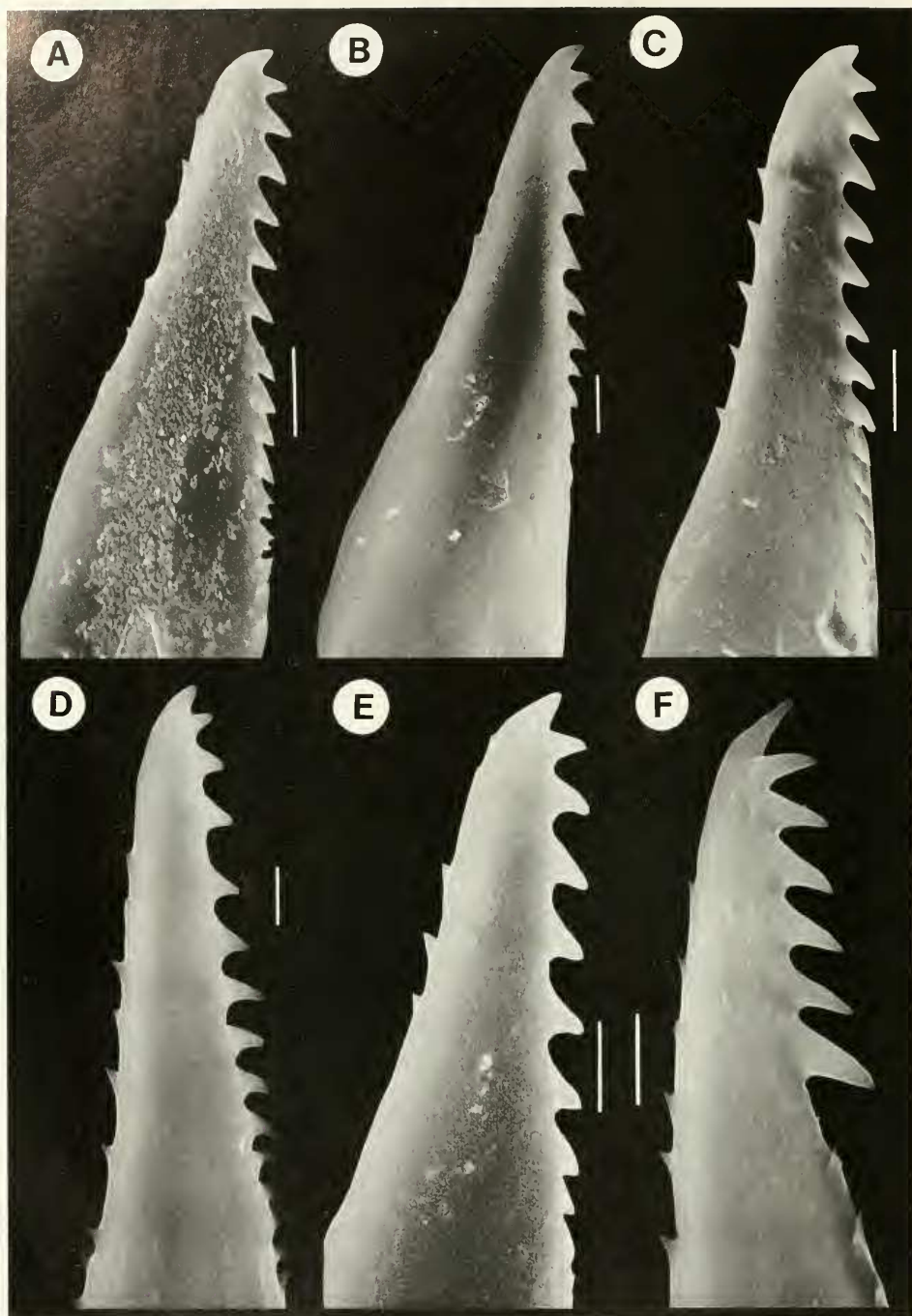


Fig. 3. SEM photomicrographs of mandibles of female. A, *Bezzia bivittata*. B, *B. imbfida*. C, *B. nobilis*. D, *B. glabra*. E, *B. dorsasetula*. F, *Phaenobezzia opaca*. White bars equal 8 μm .

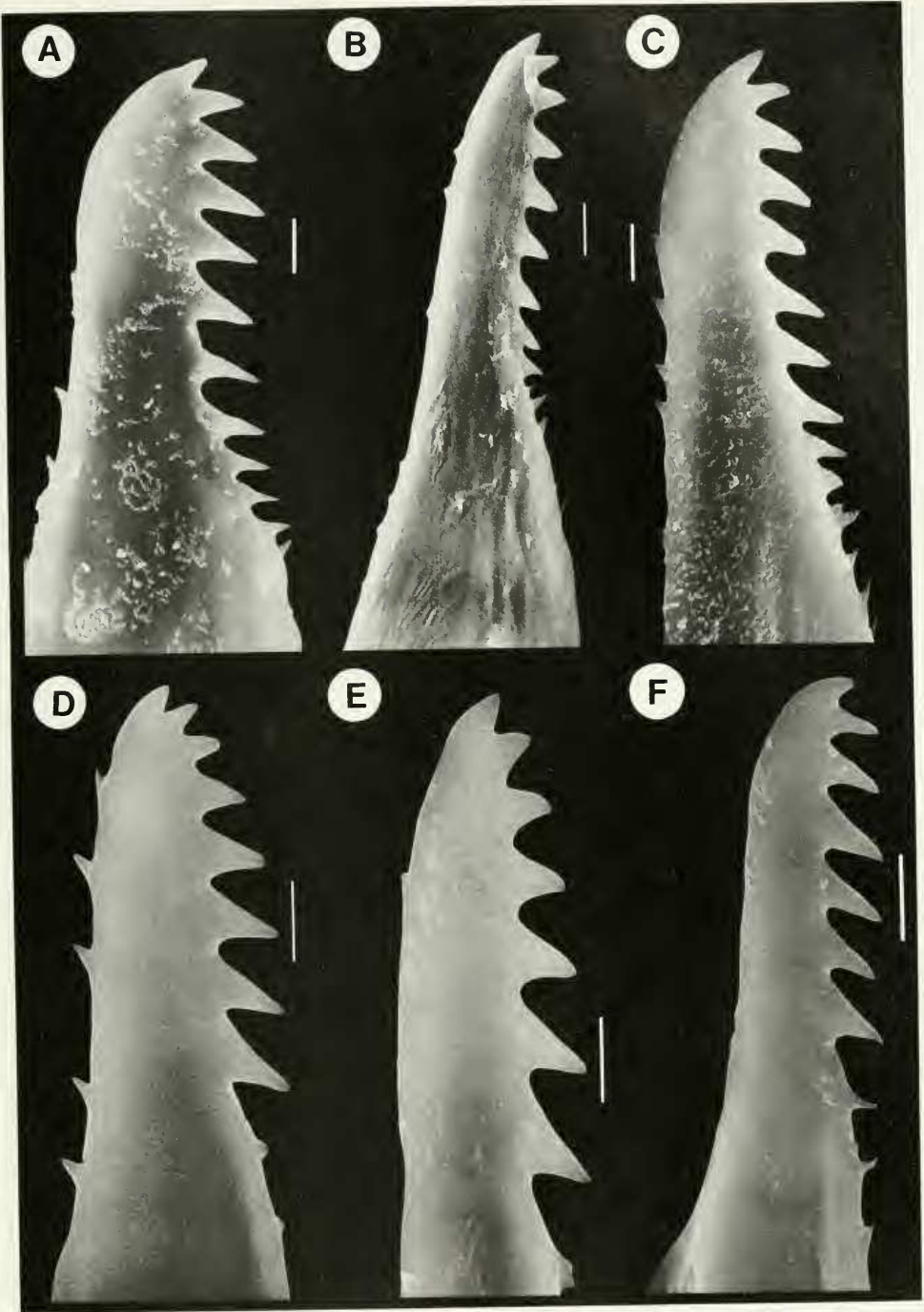


Fig. 4. SEM photomicrographs of mandibles of female. A, *Palpomyia subaspera*. B, *P. cressoni*. C, *P. lineata*. D, *P. plebeia*. E, *P. rufa*. F, *P. pseudorufa*. White bars equal 8 μm .

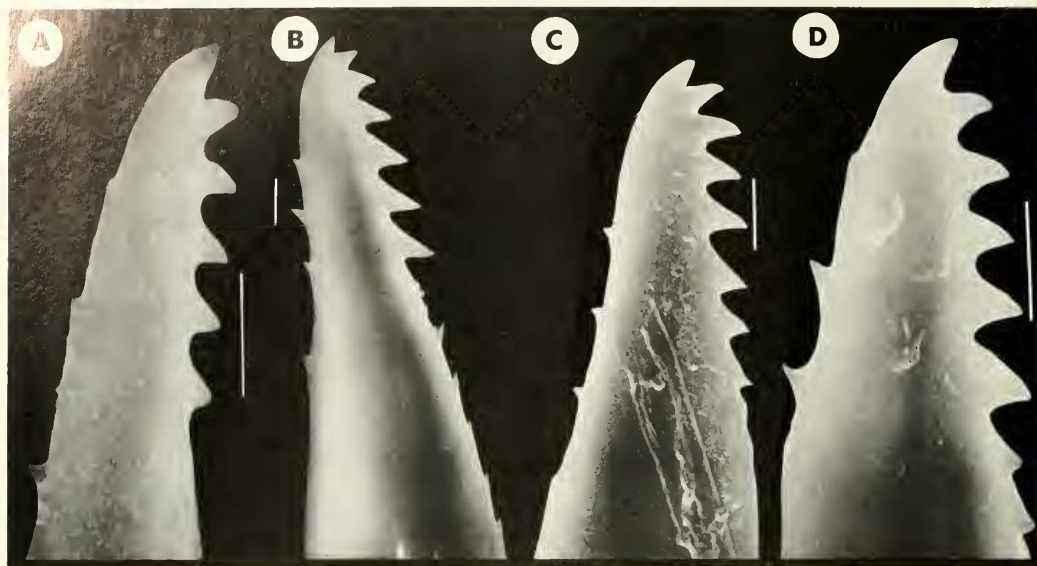


Fig. 5. SEM photomicrographs of mandibles of female. A, *Palpomyia basalis*. B, *P. flaviceps*. C, *P. scapellifera*. D, *P. hastata*. White bars equal 8 μm .

with up to 13 long, coarse, antrorse, sometimes branched, teeth on the medial edge and, in nine species, up to 10 short antrorse teeth on the lateral edge (Figs. 6–9). Maximum width is attained at approximately mid-length of the blade and is 14.1–19.3% of their total length. There is little reduction in width proximal to mid-length. The articulating mechanism of female mandibles is absent in males. The basal portion curves approximately 45° to the long axis of the blade.

Labrum.—The labrum of both sexes is moderately sclerotized, ventrally concave in cross section and proximally joined to the hypopharynx on both sides. Two short sensilla basiconica occur in pits located asymmetrically on the ventral surface near the proximal end of the row of lateral spicules (Figs. 10, 11). In females the tip is rounded and terminates in two median short, peg-like structures with rounded points; lateral to these are three, sometimes two, rounded structures. Antrorse spicules on the distal ventrolateral surface are short triangular or stout spinelike structures that occur in a sin-

gle series on each side. The labrum of males is more pointed than in conspecific females, in most species the terminal median peg-like structures are replaced by antrorse spicules, and the lateral rounded structures are reduced in size or absent. The ventrolateral spicules are longer and more slender than those of females and occur in one to three rows.

Hypopharynx.—In both sexes the moderately sclerotized hypopharynx has a deep dorsal salivary groove located above a ventral keel; both structures become less pronounced distally and terminate proximal to the tip. Antrorse spicules of varying lengths occur on the rounded or semipointed tip of the hypopharynx of females and, in most species, extend for varying distances proximally along its lateral edges. The spicules vary in shape from tooth-like to spike-like to filiform (Fig. 12). The hypopharynx of males is less heavily sclerotized, shorter and has longer spicules than those of conspecific females (Fig. 13).

Lacinia.—In both sexes of all species examined, the laciniae are acute triangular in

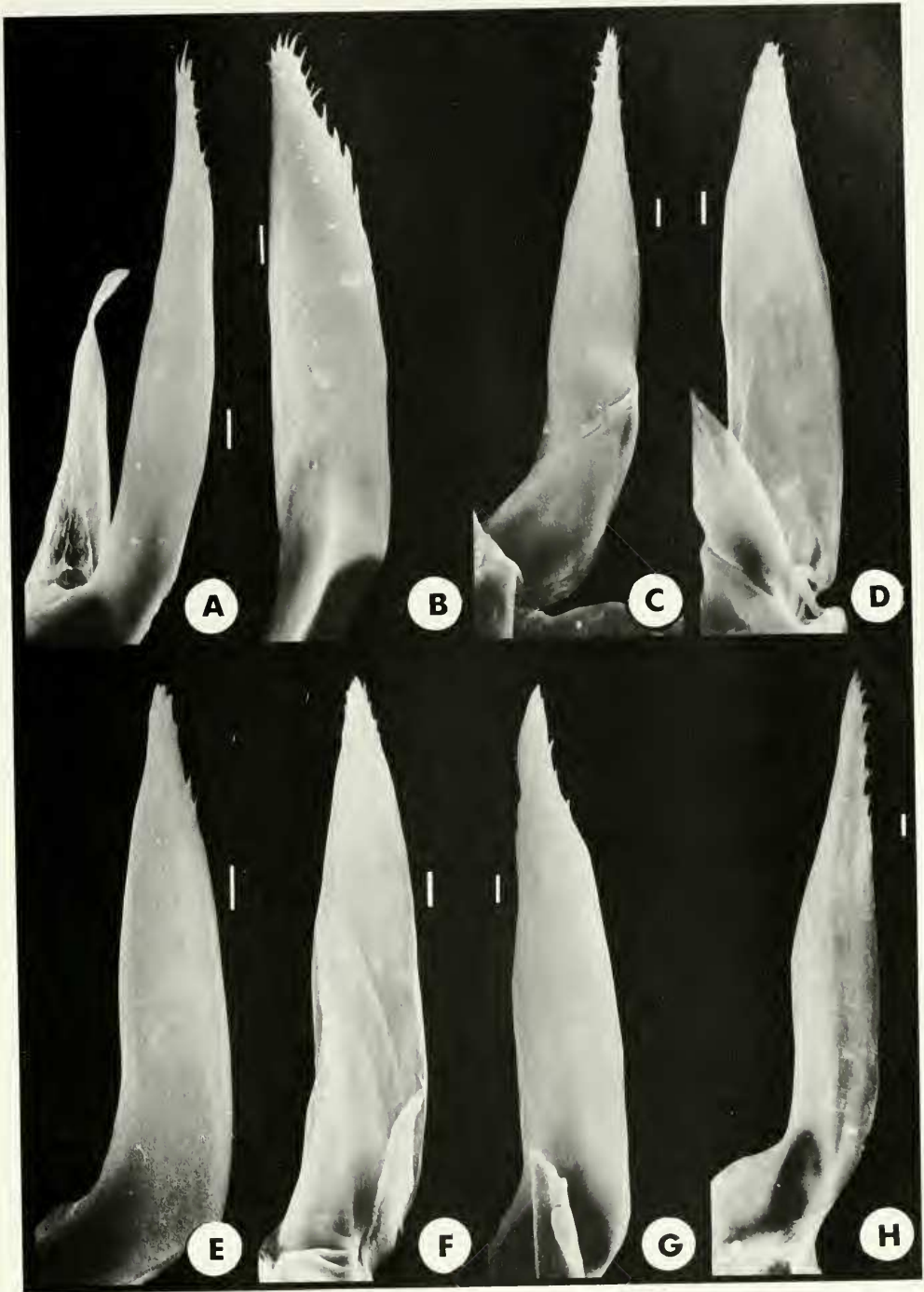


Fig. 6. SEM photomicrographs of mandibles of male. A, *Bezzia bivittata*. B, *B. imbifida*. C, *B. nobilis*. D, *B. glabra*. E, *B. dorsasetula*. F, *Phaenobezzia opaca*. G, *Palpomyia subaspera*. H, *P. lineata*. White bars equal 8 μ m.

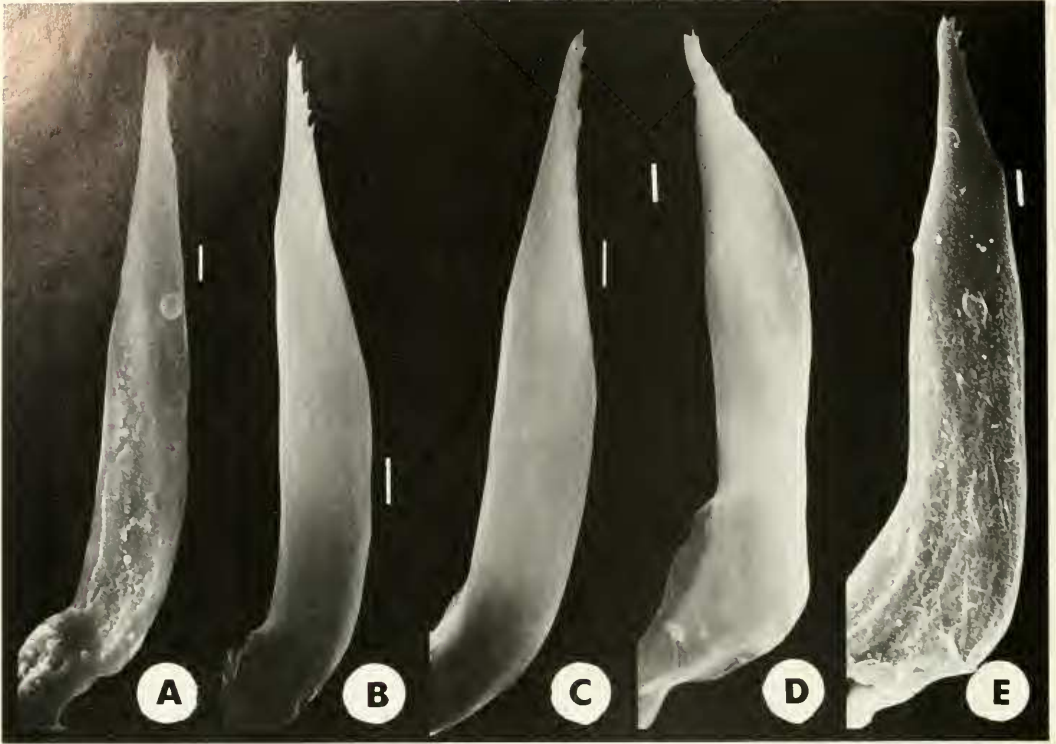


Fig. 7. SEM photomicrographs of mandibles of male. A, *Palpomyia plebeia*. B, *P. rufa*. C, *P. pseudorufa*. D, *P. basalis*. E, *P. scalpellifera*. White bars equal 8 μm .

shape, have no teeth or spicules on either the tip or edges and are one-half to three-fourths the length of the mandibles (Figs. 14–15). Their structure indicates that they serve as the lateral boundary of the proboscis food canal. The base is thick and, on broken specimens, appears to be hollow (Fig. 14C). Laciniae of both sexes of all species are similar and do not differ distinctively in appearance from each other, but females have longer laciniae than conspecific males.

Maxillary palpal sensory organ.—In both sexes of all species the filiform sensilla, known as Newstead's sensilla or bulb organs (Lewis, 1973), that constitute the sensory organ, arise from an unindented surface on the distal end of the third palpal segment as in Corethrellidae (McKeever 1986), Ceratopogonidae (McKeever et al. 1991) and Psychodidae (Brinson et al.

1993). In contrast, the sensilla arise from a pit in *Culicoides* (Chu-Wang et al. 1975) and some Ceratopogonini where the pit ranges from shallow, as in *Alluaudomyia bella* (Coquillett), to deep, with heads of the sensilla below its rim, as in *Downeshelea stonei* (Wirth) (McKeever et al. 1991). In Palpomyiini the long stalk of each sensillum originates from a recessed socket as in *Culicoides* (Rowley and Cornford 1972) and Ceratopogonini (McKeever et al. 1991) and the tip is expanded to form a head, the shape of which varies among the species (Figs. 16, 17). In some species, the sensilla are closely grouped and their heads are in approximately the same plane, but in others they originate along over half the length of the palpal segment and the stalk of one sensillum may not extend to the point of origin of a more distal one. The number of

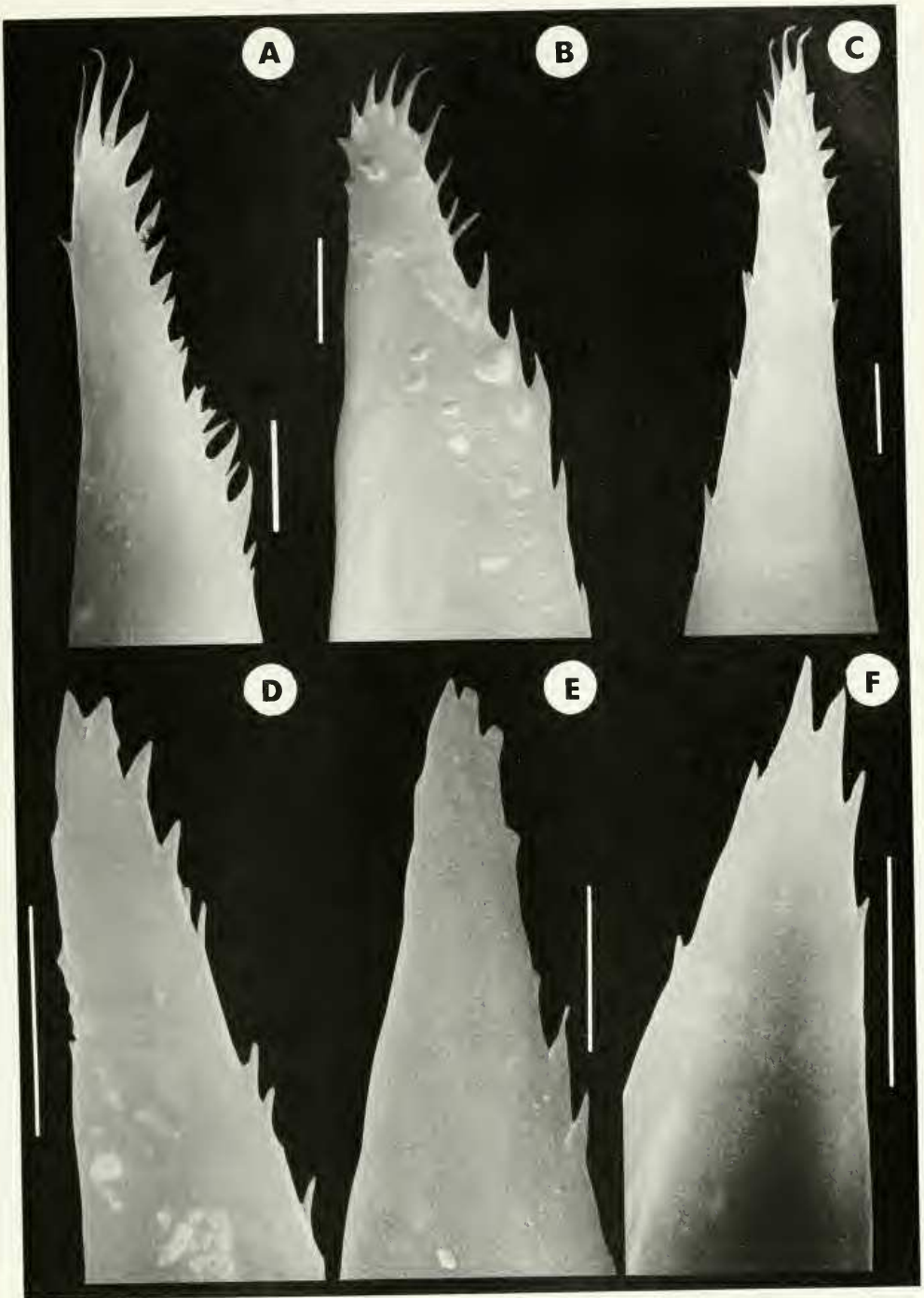


Fig. 8. SEM photomicrographs of mandibles of male. A, *Bezzia bivittata*. B, *B. imbifida*. C, *B. nobilis*. D, *B. glabra*. E, *B. dorsasetula*. F, *Phaenobezzia opaca*. White bars equal 8 μm .

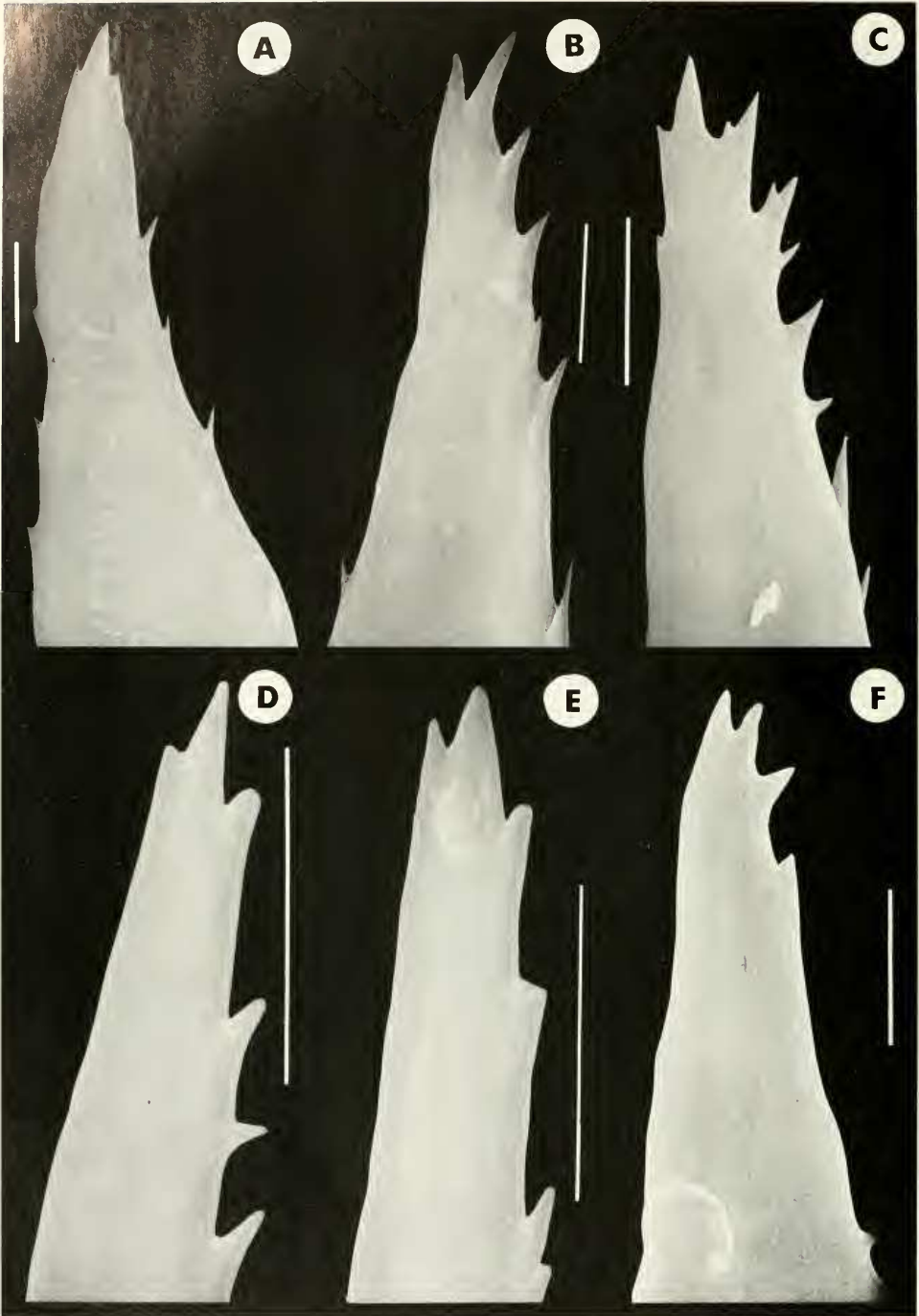


Fig. 9. SEM photomicrographs of mandibles of male. A, *Palpomyia subaspera*. B, *P. lineata*. C, *P. plebeia*. D, *P. rufa*. E, *P. pseudorufa*. F, *P. scalpellifera*. White bars equal 8 μ m.

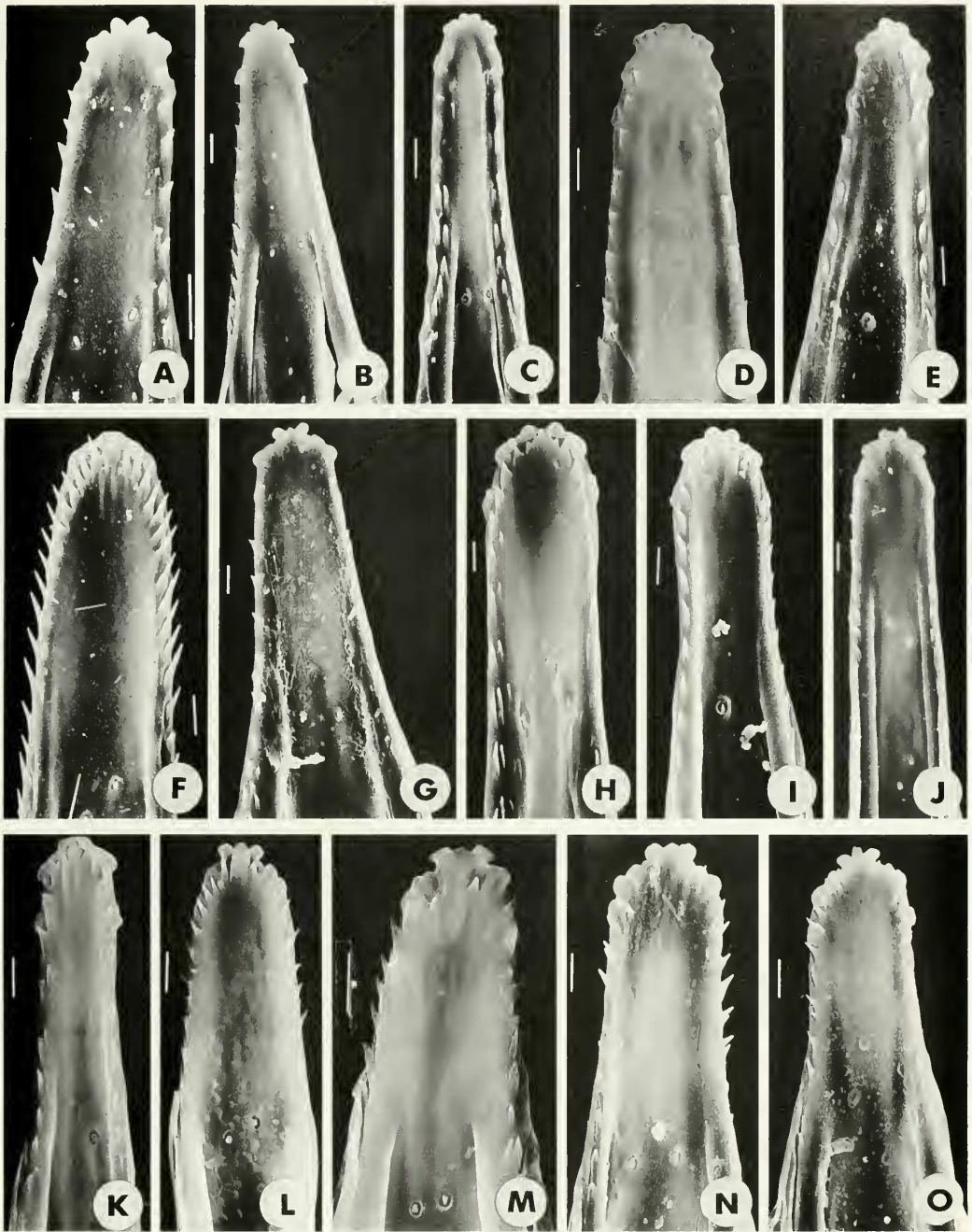


Fig. 10. SEM photomicrographs of labra of female. A, *Bezzia bivittata*. B, *B. imbrifida*. C, *B. nobilis*. D, *B. glabra*. E, *B. dorsasetula*. F, *Phaenobezzia opaca*. G, *Palpomyia cressoni*. H, *P. lineata*. I, *P. plebeia*. J, *P. rufa*. K, *P. pseudorufa*. L, *P. basalis*. M, *P. flaviceps*. N, *P. scalpellifera*. O, *P. hastata*. White bars equal 8 μ m.

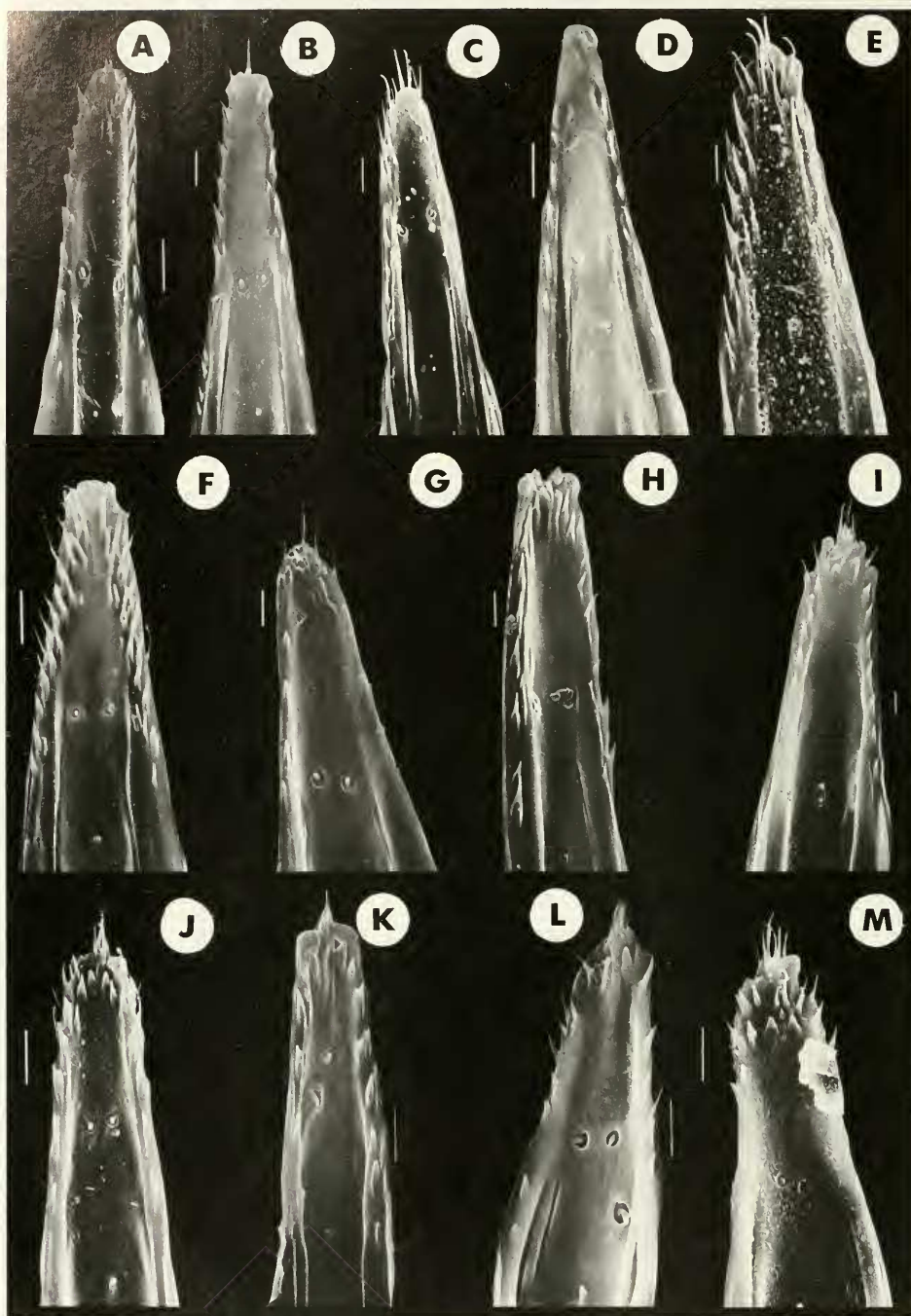


Fig. 11. SEM photomicrographs of labra of male. A, *Bezzia bivittata*. B, *B. imbrifida*. C, *B. nobilis*. D, *B. glabra*. E, *B. dorsasetula*. F, *Phaenobezzia opaca*. G, *Palpomyia subaspera*. H, *P. lineata*. I, *P. plebeia*. J, *P. rufa*. K, *P. pseudorufa*. L, *P. basalis*. M, *P. scalpellifera*. White bars equal 8 μ m.

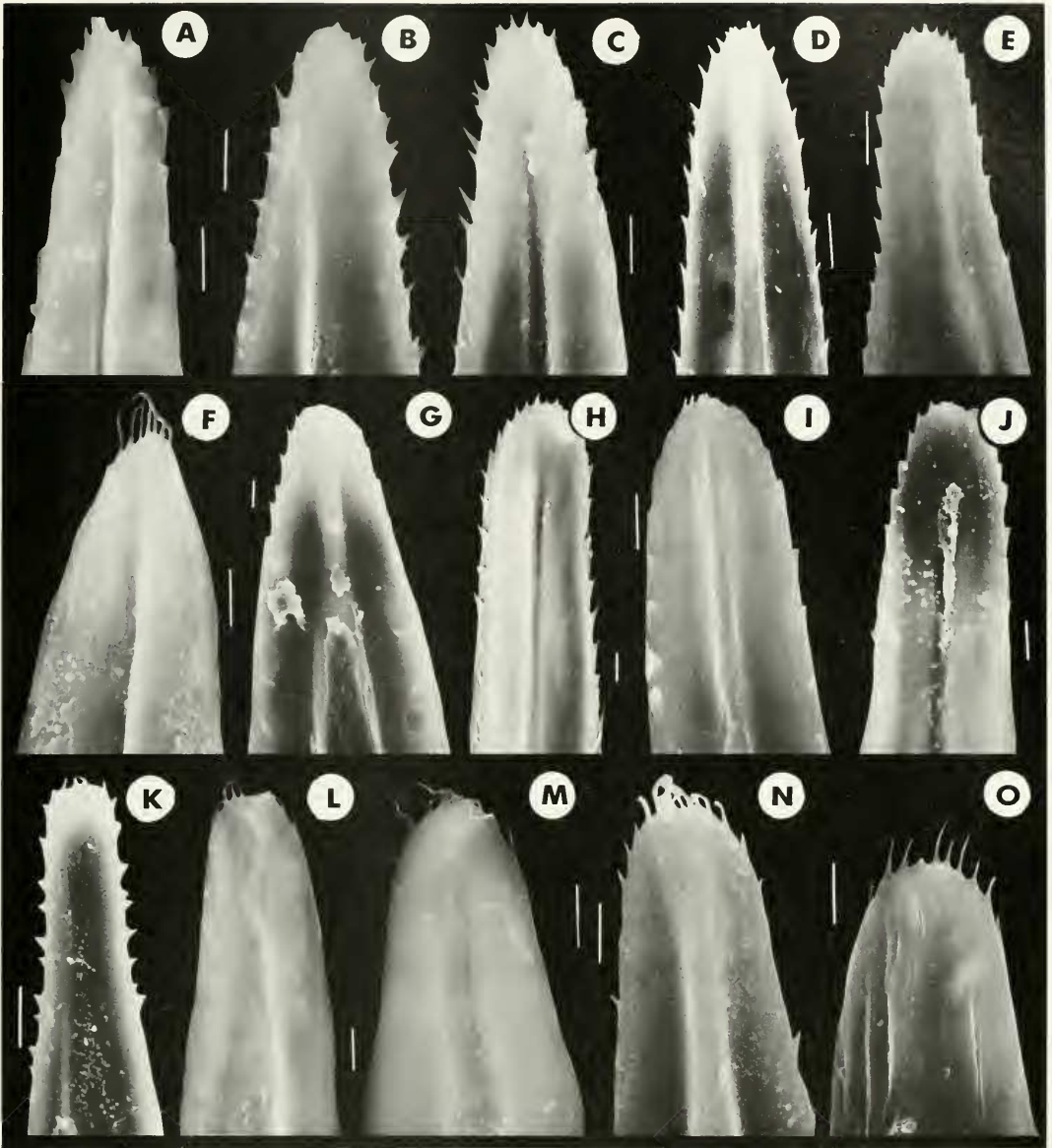


Fig. 12. SEM photomicrographs of the hypopharynx of female. A, *Bezzia bivittata*. B, *B. imbifida*. C, *B. nobilis*. D, *B. glabra*. E, *B. dorsasetula*. F, *Phaenobezzia opaca*. G, *Palpomyia cressoni*. H, *P. lineata*. I, *P. plebeia*. J, *P. rufa*. K, *P. pseudorufa*. L, *P. basalis*. M, *P. flaviceps*. N, *P. scalpellifera*. O, *P. hastata*. White bars equal 8 μm .

sensilla is approximately equal in both sexes of the same species (Tables 4, 8).

Description of Mouthparts by Species

Bezzia bivittata. Mandible (female) (Figs. 1A, 3A): 114–175 μm ($n = 13$) long, 23–37 μm ($n = 13$) wide; tooth row 23%

of total length; 7–15 ($n = 19$) small coarse medial teeth, uniform throughout, their camber 35°, pitch 71°; 0–8 ($n = 19$) small basal teeth, sometimes bifurcate; 0–6 ($n = 20$) small lateral teeth.

Mandible (male) (Figs. 6A, 8A): 121–140 μm ($n = 10$) long, 19–24 μm ($n = 10$)

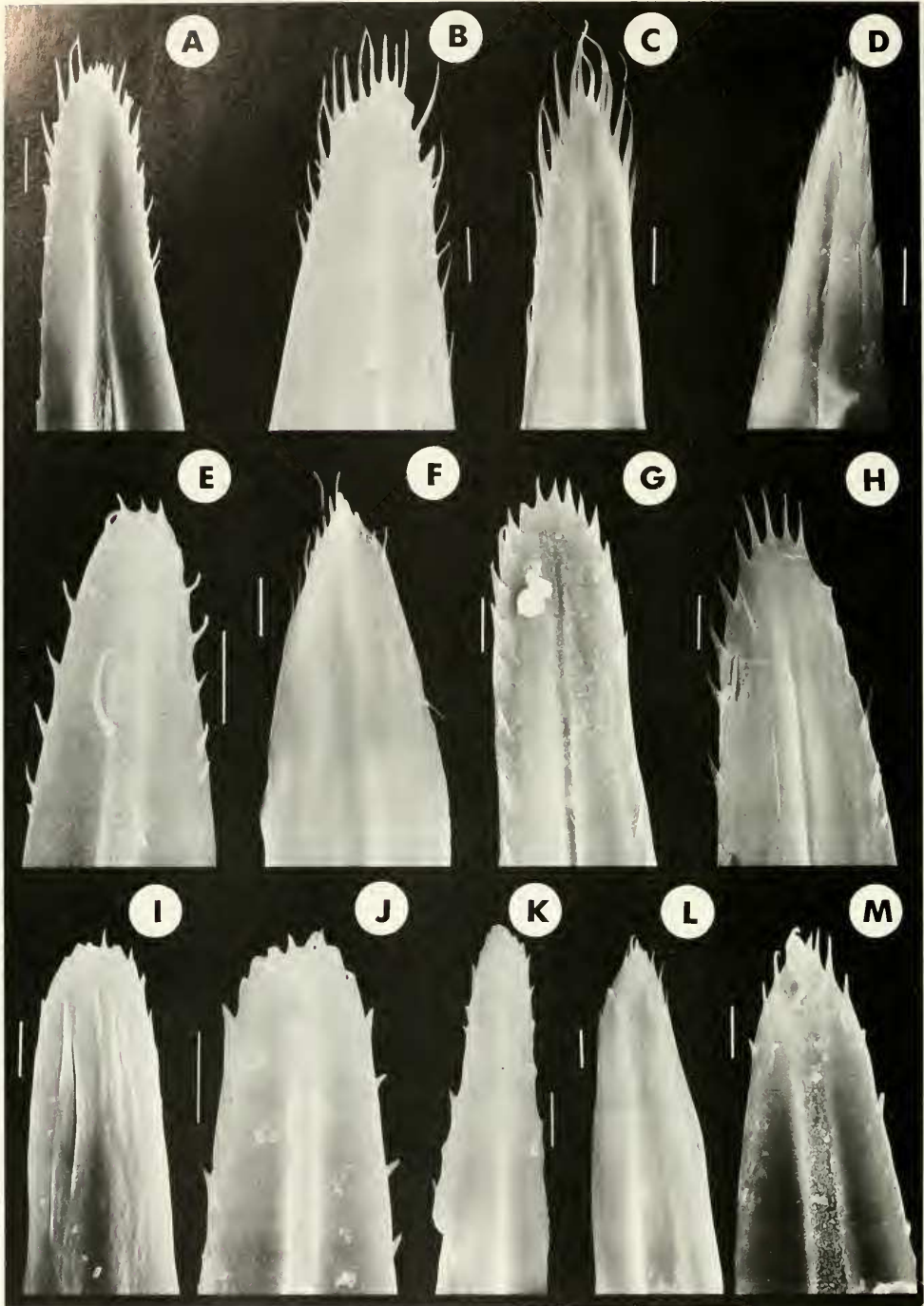


Fig. 13. SEM photomicrographs of the hypopharynx of male. A, *Bezzia bivittata*. B, *B. imbifida*. C, *B. nobilis*. D, *B. glabra*. E, *B. dorsasetula*. F, *Phaenobezzia opaca*. G, *Palpomyia subaspera*. H, *P. lineata*. I, *P. plebeia*. J, *P. rufa*. K, *P. pseudorufa*. L, *P. basalis*. M, *P. scalpellifera*. White bars equal 8 μ m.

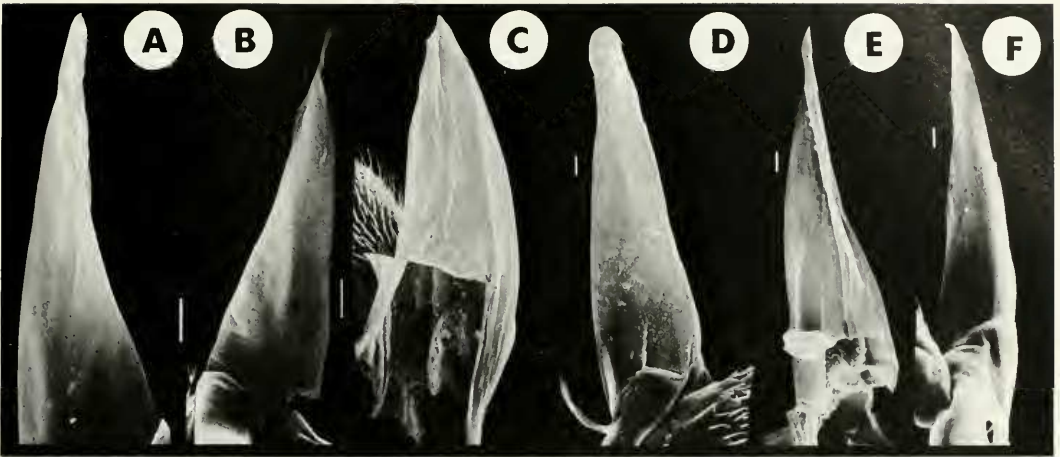


Fig. 14. SEM photomicrographs of laciniae of female. A, *Bezzia nobilis*. B, *B. dorsasetula*. C, *Phaenobezzia opaca*. D, *Palpomyia cressoni*. E, *P. lineata*. F, *P. plebeia*. White bars equal 8 μm .

wide; 4–13 ($n = 10$) large medial teeth, apical ones slender, some proximal ones may be bifurcate; 0–2 ($n = 10$) small basal teeth; 0–1 ($n = 10$) small lateral projections.

Labrum (female) (Fig. 10A): 146–189 μm ($n = 5$) long, 21–29 μm ($n = 7$) wide, 14–22 ($n = 4$) short, coarse, widely-spaced spicules.

Labrum (male) (Fig. 11A): 157–160 μm ($n = 2$) long, 16–21 μm ($n = 2$) wide; 18–20 ($n = 2$) short, coarse, widely-spaced spicules in a single row on the ventrolateral surfaces; additional row on the subapical ventral surface; spicules replace the terminal median projections of females.

Hypopharynx (female) (Fig. 12A): 142–200 μm ($n = 7$) long, 14–40 μm ($n = 7$) wide; 17–32 ($n = 4$) short, semi-blunt spicules on margins and apex.

Hypopharynx (male) (Fig. 13A): 142–186 μm ($n = 4$) long, 23–32 μm ($n = 4$) wide; 7–21 ($n = 3$) long, slender spicules on distal margins and apex, minute spicules on margins proximally.

Palpal sensory organ (female) (Fig. 16A): 3–4 ($n = 3$) closely grouped sensilla 14–15 μm ($n = 2$) long, heads spatulate.

Palpal sensory organ (male) (Fig. 17A): 2–6 ($n = 5$) closely grouped sensilla 16–19 μm ($n = 3$) long, heads spatulate.

Bezzia imbifida. Mandible (female) (Figs. 1B, 3B): 158–182 μm ($n = 11$) long, 27–35 μm ($n = 12$) wide; tooth row 24% of total length; 7–12 ($n = 12$) small, coarse medial teeth, diminishing in size proximally, their camber 25°, pitch 75°; 1–4 ($n = 12$) small, basal teeth; 3–6 ($n = 12$) minute lateral teeth.

Mandible (male) (Figs. 6B, 8B): 134–165 μm ($n = 10$) long, 20–23 μm ($n = 10$) wide; 6–11 ($n = 11$) large medial teeth, apical ones slender, proximal ones coarse; 0–2 ($n = 11$) small basal teeth; 0–3 ($n = 11$) minute lateral teeth.

Labrum (female) (Fig. 10B): 176–180 μm ($n = 2$) long, 28–29 μm ($n = 5$) wide; 20–30 μm ($n = 5$) coarse, closely spaced spicules.

Labrum (male) (Fig. 11B): 152–169 μm ($n = 4$) long, 19–21 μm ($n = 6$) wide; 17 ($n = 1$) sharp, widely-spaced spicules on the ventrolateral surfaces and as replacements for the median projections of females.

Hypopharynx (female) (Fig. 12B): 177–178 μm ($n = 3$) long, 19–25 μm ($n = 6$) wide; 17–22 ($n = 6$) short, sharp, irregularly spaced spicules on lateral margins, and sparse, irregularly spaced projections on apex.

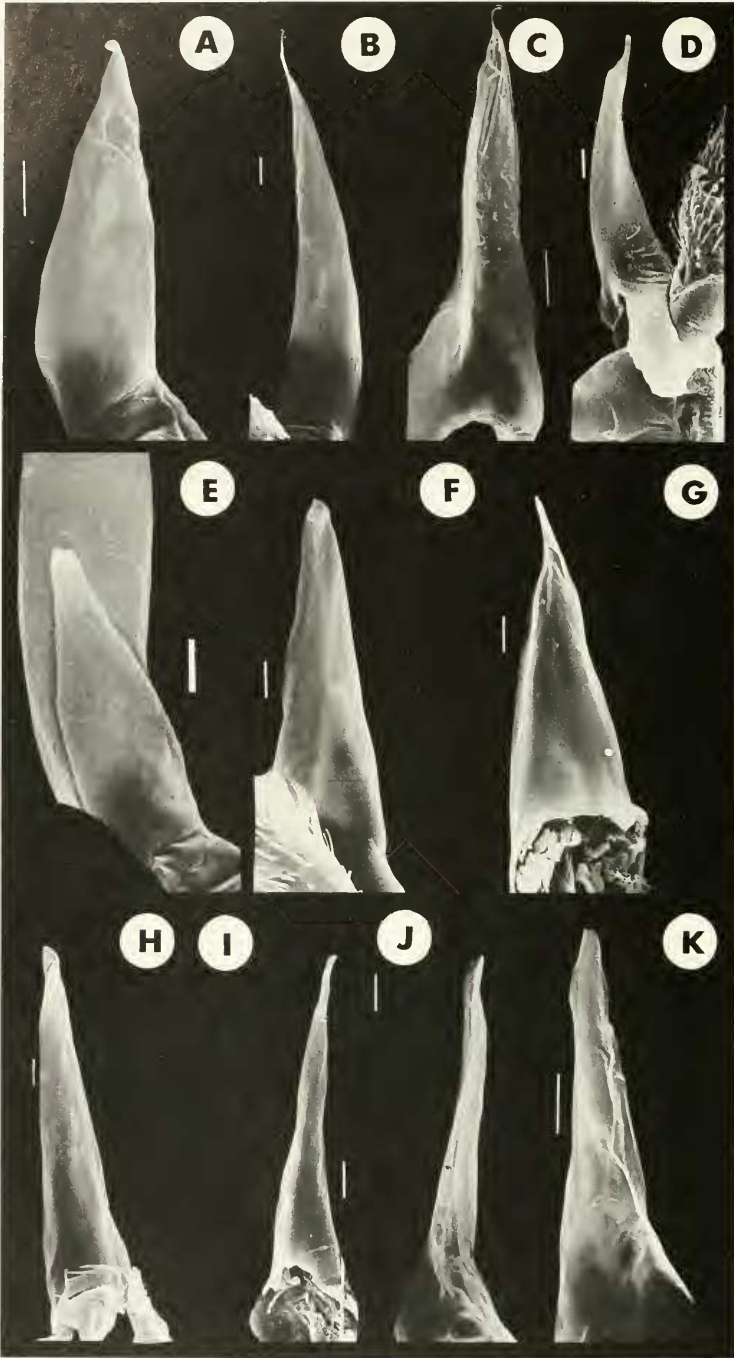


Fig. 15. SEM photomicrographs of laciniae of male. A, *Bezzia bivittata*. B, *B. imbifida*. C, *B. glabra*. D, *B. dorsasetula*. E, *Phaenobezzia opaca*. F, *Palpomyia subaspera*. G, *P. lineata*. H, *P. plebeia*. I, *P. rufa*. J, *P. pseudorufa*. K, *P. scalpellifera*. White bars equal 8 μ m.

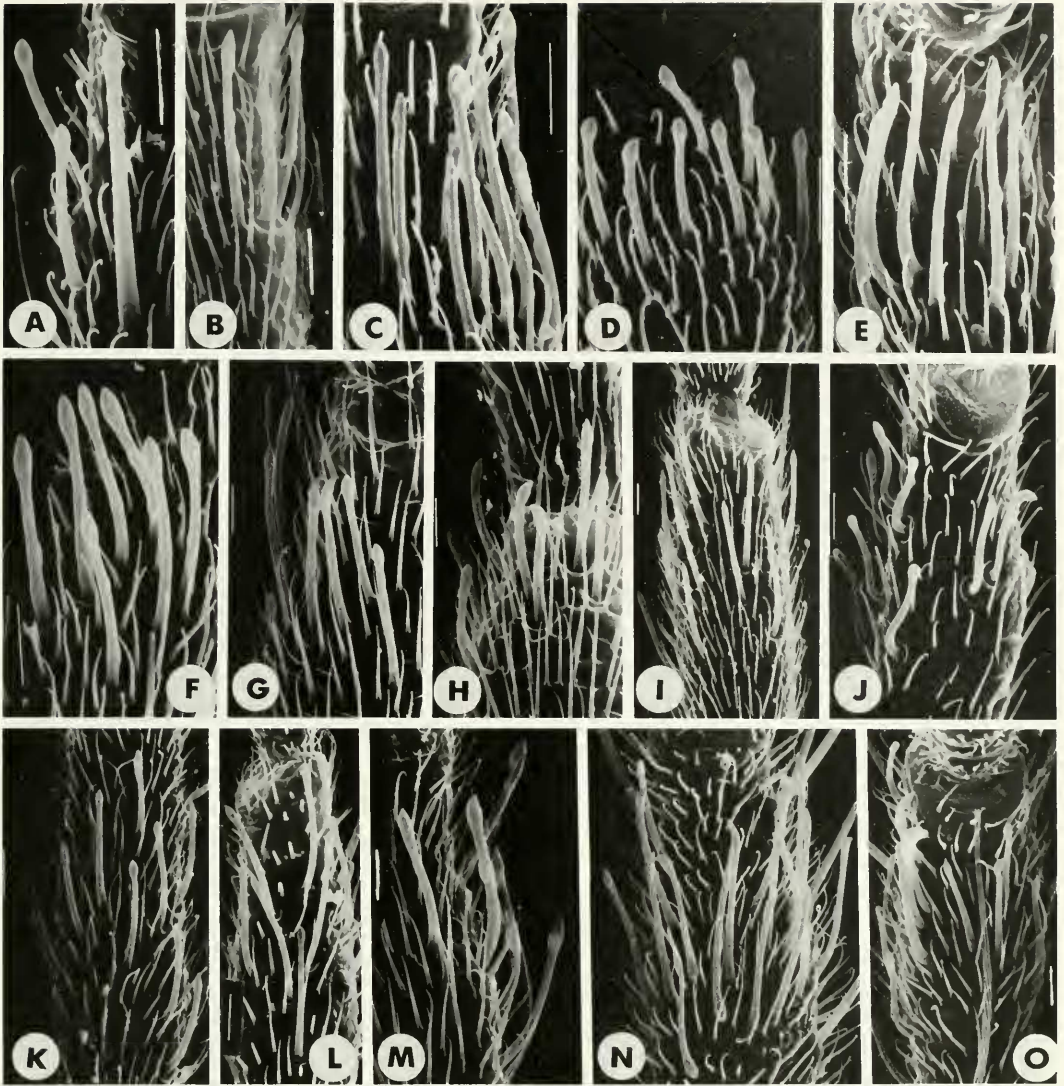


Fig. 16. SEM photomicrographs of sensilla of female. A, *Bezzia bivittata*. B, *B. imbfida*. C, *B. nobilis*. D, *B. glabra*. E, *B. dorsasetula*. F, *Phaenobezzia opaca*. G, *Palpomyia subaspera*. H, *P. cressoni*. I, *P. lineata*. J, *P. plebeia*. K, *P. rufa*. L, *P. pseudorufa*. M, *P. flaviceps*. N, *P. scalpellifera*. O, *P. hastata*. White bars equal 8 μm .

Hypopharynx (male) (Fig. 13B): 153–168 μm ($n = 3$) long, 19–20 μm ($n = 4$) wide; 11–21 ($n = 4$) long, slender, closely spaced spicules on distal margins and apex.

Palpal sensory organ (female) (Fig. 16B): 5–8 ($n = 7$) closely grouped sensilla 37.5–37.5 μm ($n = 3$) long, heads spatulate.

Palpal sensory organ (male) (Fig. 17B):

4–7 ($n = 5$) closely grouped sensilla 16–19 μm ($n = 4$) long, heads spatulate.

Bezzia nobilis. Mandible (female) (Figs. 1C, 3C): 142–196 μm ($n = 34$) long, 31–96 μm ($n = 37$) wide; tooth row 30% of total length; 7–10 μm ($n = 45$) large coarse medial teeth, diminishing in size proximally, their camber 32°, pitch 71°; 0–8 ($n =$

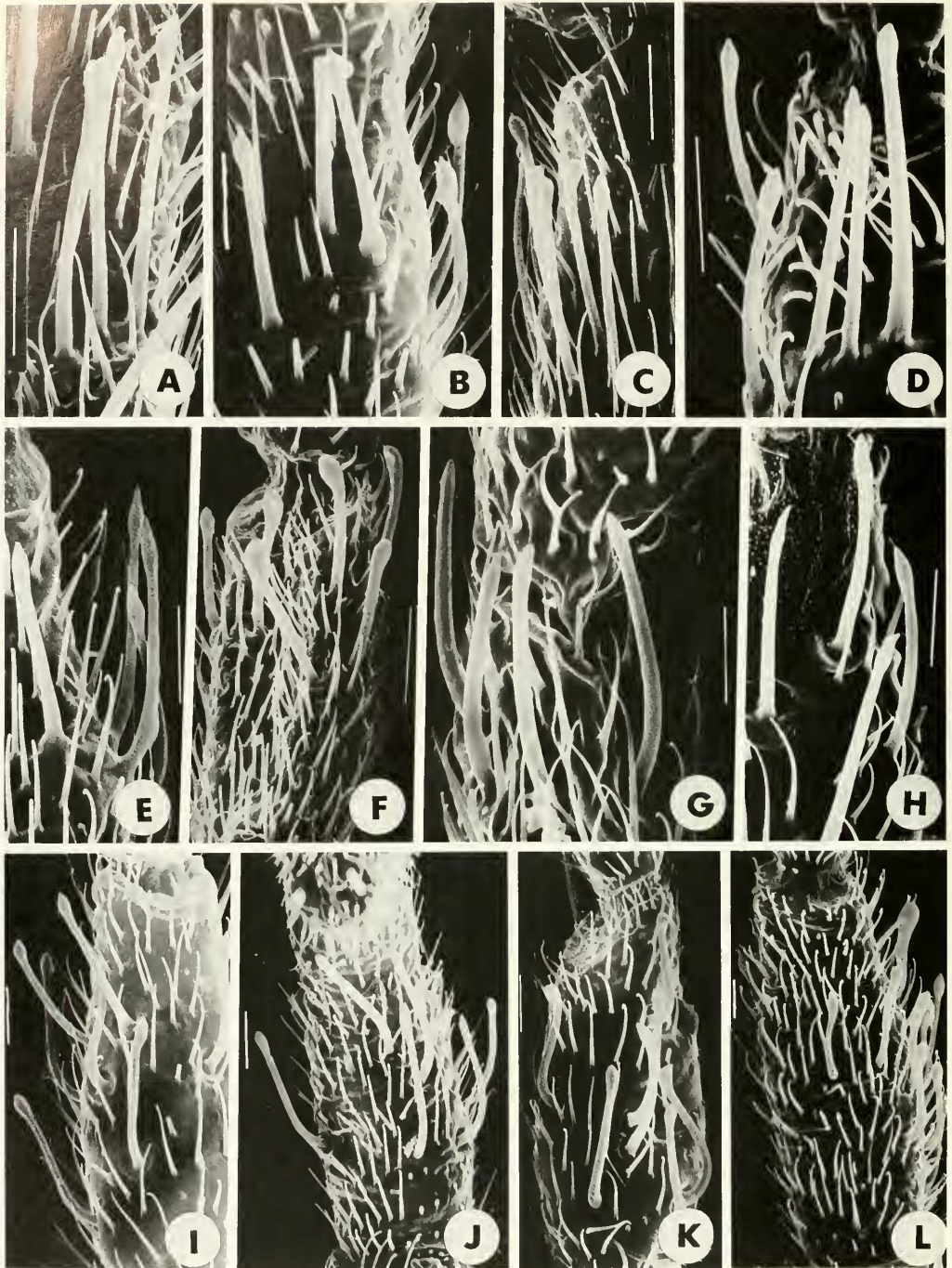


Fig. 17. SEM photomicrographs of sensilla of male. A, *Bezzia bivittata*. B, *B. imbrifida*. C, *B. nobilis*. D, *B. glabra*. E, *B. dorsasetula*. F, *Phaenobezzia opaca*. G, *Palpomyia subaspera*. H, *P. lineata*. I, *P. plebeia*. J, *P. rufa*. K, *P. pseudorufa*. L, *P. scalpellifera*. White bars equal 8 μ m.

Table 4. Measurements (μm) of laciniae and measurements and number of sensilla of maxillary palpal sensory organ of female *Palpomyiini*.

Species	Laciniae						Sensilla					
	Total Length			Maximum Width			No. per Organ			Total Length		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
<i>B. bivittata</i>	105.51	10.94	6	26.38	1.37	6	3.67	1.43	3	14.75	—	2
<i>B. imbifida</i>	106.90	7.47	8	26.27	1.95	8	6.14	1.41	7	37.50	—	3
<i>B. nobilis</i>	115.42	5.02	14	29.79	2.29	15	6.87	1.06	16	19.40	1.55	5
<i>B. glabra</i>	91.77	20.08	4	26.27	9.52	4	5.37	1.20	16	11.20	0.71	6
<i>B. dorsasetula</i>	83.09	3.63	19	25.62	0.70	16	5.42	0.43	24	19.80	2.03	5
<i>Ph. opaca</i>	81.36	5.23	18	29.65	1.89	27	6.60	0.72	15	18.47	1.85	6
<i>P. subaspera</i>	127.68	—	2	43.22	—	2	10.00	—	1	26.50	3.68	6
<i>P. cressoni</i>	142.58	21.57	5	39.37	3.80	5	7.43	1.18	7	21.83	2.24	6
<i>P. lineata</i>	110.83	76.30	3	30.15	24.35	3	12.00	—	1	28.53	2.81	6
<i>P. plebeia</i>	115.49	5.39	18	28.21	2.13	14	7.85	1.01	13	16.50	1.72	6
<i>P. rufa</i>	154.92	8.67	19	36.48	2.58	19	8.05	1.34	18	17.83	1.23	6
<i>P. pseudorufa</i>	121.47	12.74	9	25.77	1.96	9	5.29	0.51	17	20.80	0.55	5
<i>P. basalis</i>	—	—	0	—	—	0	—	—	0	—	—	0
<i>P. flaviceps</i>	97.62	24.42	5	27.04	16.63	3	5.53	0.77	17	28.00	2.77	5
<i>P. scalpellifera</i>	130.78	50.04	3	37.68	15.61	3	9.80	3.56	5	30.85	1.42	5
<i>P. hastata</i>	—	—	0	—	—	0	12.00	—	1	20.34	3.07	5

45) small, basal teeth; 2–8 ($n = 45$) prominent lateral teeth.

Mandible (male) (Figs. 6C, 8C): 120–169 μm ($n = 12$) long, 20–32 μm ($n = 15$) wide; 2–13 ($n = 15$) small short medial teeth, apical ones long and slender; 0–4 ($n = 15$) minute basal teeth; 0–3 ($n = 15$)

minute lateral teeth, proximal ones short, apical ones long and slender.

Labrum (female) (Fig. 10C): 146–225 μm ($n = 18$) long, 23–40 μm ($n = 20$) wide; 17–30 ($n = 7$) coarse, closely spaced spicules in single row distally and double row proximally on ventrolateral surfaces.

Table 5. Measurements (μm) of mandibles of male *Palpomyiini*.

Species	Total Length			Maximum Width			Width at Basal Tooth			Length of Tooth Row		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
<i>B. bivittata</i>	133.93	6.18	10	21.28	1.42	10	12.05	2.99	10	25.80	6.95	10
<i>B. imbifida</i>	147.92	8.06	9	20.80	0.72	11	11.95	0.73	11	33.12	6.03	11
<i>B. nobilis</i>	147.63	8.89	12	25.36	2.30	15	9.84	2.44	15	26.60	8.79	15
<i>B. glabra</i>	138.54	9.77	6	25.67	1.42	10	7.00	2.06	10	14.89	5.55	10
<i>B. dorsasetula</i>	114.61	2.14	17	21.87	1.35	18	11.90	0.95	18	22.24	2.72	18
<i>Ph. opaca</i>	118.51	6.14	18	24.80	1.54	20	10.83	1.29	20	17.86	2.63	20
<i>P. subaspera</i>	130.34	10.38	5	25.05	2.71	6	13.60	0.93	7	30.02	5.40	7
<i>P. cressoni</i>	—	—	0	—	—	0	—	—	0	—	—	0
<i>P. lineata</i>	146.30	11.17	14	26.78	2.52	15	11.53	1.92	15	23.76	5.46	15
<i>P. plebeia</i>	118.59	2.31	18	20.02	1.31	18	7.54	1.04	18	15.81	1.60	18
<i>P. rufa</i>	134.42	8.02	15	22.34	1.65	15	10.02	1.07	15	21.55	3.58	15
<i>P. pseudorufa</i>	113.37	3.89	22	20.31	0.80	22	7.50	0.43	22	21.70	1.71	22
<i>P. basalis</i>	105.07	—	2	19.95	—	2	—	—	0	—	—	0
<i>P. flaviceps</i>	—	—	0	—	—	0	—	—	0	—	—	0
<i>P. scalpellifera</i>	117.05	25.89	4	22.61	1.75	4	7.98	5.18	4	13.30	9.30	4
<i>P. hastata</i>	—	—	0	—	—	0	—	—	0	—	—	0

Table 6. Measurements (μm) and number of spicules of mandibles of male *Palpomyiini*.

Species	Length of Longest Tooth			No. of Coarse Medial Teeth			No. of Small Basal Teeth			No. of Lateral Teeth		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
<i>B. bivittata</i>	1.92	0.53	9	7.40	2.06	10	0.20	0.45	10	0.70	0.23	10
<i>B. imbibida</i>	2.71	0.12	12	8.36	1.24	11	0.36	0.54	11	0.45	0.70	11
<i>B. nobilis</i>	4.41	0.27	39	5.87	1.61	15	0.67	0.77	15	0.40	0.50	15
<i>B. glabra</i>	5.19	0.44	26	4.30	1.58	10	0.50	0.61	10	0.20	0.30	10
<i>B. dorsasetula</i>	1.92	0.41	18	5.94	0.47	18	0.00	—	18	0.00	—	18
<i>Ph. opaca</i>	2.24	0.47	19	4.10	0.60	20	0.00	—	20	0.55	0.72	20
<i>P. subaspera</i>	1.90	0.66	7	4.14	1.55	7	—	—	0	0.71	0.66	7
<i>P. cressoni</i>	—	—	0	—	—	0	—	—	0	—	—	0
<i>P. lineata</i>	2.75	0.59	15	5.94	1.00	16	0.31	0.42	16	0.19	0.29	16
<i>P. plebeia</i>	1.81	0.37	18	5.00	1.11	18	0.00	—	18	0.17	0.26	18
<i>P. rufa</i>	2.08	0.57	15	4.80	0.70	15	0.27	0.57	15	0.00	—	14
<i>P. pseudorufa</i>	1.99	0.27	22	4.86	0.31	22	0.00	—	22	0.00	—	22
<i>P. basalis</i>	—	—	0	—	—	0	—	—	0	—	—	0
<i>P. flaviceps</i>	—	—	0	—	—	0	—	—	0	—	—	0
<i>P. scalpellifera</i>	1.33	0	4	4.25	2.00	4	0.00	—	4	0.00	—	4
<i>P. hastata</i>	—	—	0	—	—	0	—	—	0	—	—	0

Labrum (male) (Fig. 11C): 160–186 μm ($n = 7$) long, 20–27 μm ($n = 8$) wide, 16–29 ($n = 8$) spicules, the proximal ones coarse, distal ones long and slender.

Hypopharynx (female) (Fig. 12C): 165–229 μm ($n = 16$) long, 22–37 μm ($n = 17$) wide; 15–46 ($n = 11$) short, sharp, irregularly spaced spicules on lateral margins and apex.

Hypopharynx (male) (Fig. 13C): 172–184 μm ($n = 7$) long, 17–33 μm ($n = 8$) wide; 11–22 ($n = 6$) long, slender, closely spaced spicules on distal margins and apex.

Palpal sensory organ (female) (Fig. 16C): 2–10 ($n = 16$) closely grouped sensilla 17–21 μm ($n = 5$) long, heads spatulate.

Palpal sensory organ (male) (Fig. 17C):

Table 7. Measurements (μm) and number of spicules of labra and hypopharynx of male *Palpomyiini*.

Species	Labra						Hypopharynx					
	Total Length			No. of Spicules			Total Length			No. of Spicules		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
<i>B. bivittata</i>	158.27	—	2	19.00	—	2	159.27	29.99	4	13.33	17.62	3
<i>B. imbibida</i>	158.60	11.77	4	17.00	—	1	159.15	18.79	3	16.50	6.69	4
<i>B. nobilis</i>	173.09	8.33	7	21.75	3.81	8	176.89	4.49	7	16.32	3.91	6
<i>B. glabra</i>	154.72	8.31	3	14.00	3.04	5	159.27	21.04	4	13.33	2.87	6
<i>B. dorsasetula</i>	142.16	4.75	9	18.67	4.28	6	139.92	4.59	9	15.87	1.92	8
<i>Ph. opaca</i>	141.74	11.09	7	22.75	6.79	8	137.39	9.76	10	12.12	2.66	8
<i>P. subaspera</i>	147.30	5.57	4	18.67	5.74	3	147.63	11.45	3	13.50	—	2
<i>P. cressoni</i>	—	—	0	—	—	0	—	—	0	—	—	0
<i>P. lineata</i>	171.57	22.18	5	15.50	4.78	6	175.12	15.71	6	13.30	3.36	6
<i>P. plebeia</i>	144.78	6.68	7	18.71	2.65	7	139.65	7.75	6	13.30	1.47	10
<i>P. rufa</i>	160.40	10.64	10	14.25	2.08	8	162.09	15.44	8	11.50	5.40	8
<i>P. pseudorufa</i>	129.01	6.88	8	11.11	2.29	9	129.01	5.07	11	14.82	1.46	11
<i>P. basalis</i>	143.64	—	1	16.00	—	1	140.98	—	1	11.00	—	1
<i>P. flaviceps</i>	—	—	0	—	—	0	—	—	0	—	—	0
<i>P. scalpellifera</i>	133.00	—	1	11.00	—	1	131.67	—	1	4.00	—	1
<i>P. hastata</i>	—	—	0	—	—	0	—	—	0	—	—	0

Table 8. Measurements (μm) of laciniae and measurements and number of sensilla of maxillary palpal sensory organ of male *Palpomyiini*.

Species	Laciniae						Sensilla					
	Total Length			Maximum Width			No. per Organ			Total Length		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
<i>B. bivittata</i>	88.78	16.51	4	23.61	7.60	4	3.40	2.08	5	17.48	2.79	3
<i>B. imbifida</i>	95.91	3.45	9	20.17	2.85	6	5.50	2.05	5	16.93	1.75	4
<i>B. nobilis</i>	100.50	10.30	10	21.52	3.06	11	4.25	0.86	12	17.86	0.88	4
<i>B. glabra</i>	55.33	13.84	5	17.73	9.54	3	2.78	1.00	9	15.16	2.70	5
<i>B. dorsasetula</i>	72.61	5.18	10	20.21	2.36	10	4.25	0.87	8	19.73	2.28	3
<i>Ph. opaca</i>	73.15	9.94	7	23.37	3.00	7	4.22	0.71	18	11.29	0.87	4
<i>P. subaspera</i>	82.46	5.65	6	23.05	5.41	5	4.17	1.68	6	21.06	2.13	4
<i>P. cressoni</i>	—	—	0	—	—	0	—	—	0	—	—	0
<i>P. lineata</i>	85.56	5.09	9	28.50	3.61	7	3.86	0.64	7	17.17	0.00	3
<i>P. plebeia</i>	86.24	2.70	13	22.30	1.28	13	4.50	0.63	14	19.33	2.67	14
<i>P. rufa</i>	91.27	8.86	8	19.42	2.78	5	3.85	0.69	13	17.60	2.12	5
<i>P. pseudorufa</i>	79.92	3.44	11	15.23	1.16	11	3.00	0.59	18	19.39	1.96	5
<i>P. basalis</i>	—	—	0	—	—	0	—	—	0	—	—	0
<i>P. flaviceps</i>	—	—	0	—	—	0	—	—	0	—	—	0
<i>P. scalpellifera</i>	91.77	—	1	35.90	—	1	8.00	—	2	18.40	0.74	5
<i>P. hastata</i>	—	—	0	—	—	0	—	—	0	—	—	0

2–6 ($n = 12$) closely grouped sensilla 17–18 μm ($n = 4$) long, heads spatulate.

Bezzia glabra. Mandible (female) (Figs. 1D, 3D): 148–226 μm ($n = 24$) long, 28–50 μm ($n = 26$) wide; tooth row 28% of total length; 7–17 μm ($n = 27$) medium size medial teeth, diminishing in size proximally, distal ones widely spaced, their camber 43°, pitch 89°; 0–4 ($n = 27$) small, basal teeth; 0–10 ($n = 27$) small to prominent lateral teeth.

Mandible (male) (Figs. 6D, 8D): 128–149 μm ($n = 6$) long, 23–29 μm ($n = 10$) wide; 2–10 ($n = 10$) small to medium medial teeth, proximal ones slender; 0–2 ($n = 10$) minute basal teeth; 0–1 ($n = 10$) minute lateral teeth.

Labrum (female) (Fig. 10D): 169–269 μm ($n = 11$) long, 29–43 μm ($n = 11$) wide; 12–29 ($n = 11$) coarse, closely spaced spicules.

Labrum (male) (Fig. 11D): 152–158 μm ($n = 3$) long, 21–28 μm ($n = 6$) wide, 11–17 ($n = 5$) coarse spicules on the anteroventral surfaces, apex without spicules, similar to that of females, but structures less developed.

Hypopharynx (female) (Fig. 12D): 186–

274 μm ($n = 12$) long, 20–39 μm ($n = 12$) wide; 6–37 ($n = 11$) short, sharp, widely and regularly spaced spicules on lateral margins and apex.

Hypopharynx (male) (Fig. 13D): 149–178 μm ($n = 4$) long, 13–16 μm ($n = 5$) wide; 9–16 ($n = 6$) long, slender closely spaced spicules on most distal margins and apex, short spicules on margins proximally.

Palpal sensory organ (female) (Fig. 16D): 1–9 ($n = 15$) closely grouped sensilla 10–12 μm ($n = 6$) long, heads spatulate.

Palpal sensory organ (male) (Fig. 17D): 1–5 ($n = 9$) closely grouped sensilla 13–18 μm ($n = 5$) long, heads spatulate.

Bezzia dorsasetula. Mandible (female) (Figs. 1E, 3D): 116–144 μm ($n = 33$) long, 24–32 μm ($n = 35$) wide; tooth row 23% of total length; 6–9 ($n = 31$) large coarse medial teeth, distal ones uniform, proximal ones progressively smaller, their camber 35°, pitch 85°; 0–5 ($n = 31$) small basal teeth; 2–7 ($n = 33$) prominent lateral teeth.

Mandible (male) (Figs. 6E, 8E): 106–120 μm ($n = 17$) long, 20–31 μm ($n = 18$) wide; 4–7 ($n = 8$) medium medial teeth, lateral teeth absent.

Labrum (female) (Fig. 10E): 149–172

μm ($n = 15$) long, 21–27 μm ($n = 17$) wide; 12–23 ($n = 12$) coarse, closely spaced spicules.

Labrum (male) (Fig. 11E): 134–153 μm ($n = 9$) long, 17–24 μm ($n = 9$) wide, 15–26 ($n = 6$) long, slender spicules in 2–3 rows on the ventrolateral surfaces and apex, apical structures of females absent.

Hypopharynx (female) (Fig. 12E): 133–169 μm ($n = 17$) long, 20–24 μm ($n = 18$) wide; 18–24 ($n = 14$) very short, regularly and widely spaced spicules on lateral margins, those on the rounded apex closely spaced.

Hypopharynx (male) (Fig. 13E): 133–150 μm ($n = 9$) long, 15–20 μm ($n = 10$) wide; 12–19 ($n = 8$) short, widely and evenly spaced spicules on margins and apex.

Palpal sensory organ (female) (Fig. 16E): 3–8 ($n = 24$) closely grouped sensilla 18–22 μm ($n = 5$) long, heads filiform.

Palpal sensory organ (male) (Fig. 17E): 3–5 ($n = 8$) closely grouped sensilla 19–20 μm ($n = 3$) long, heads fusiform.

Phaenobezzia opaca. Mandible (female) (Figs. 1F, 3F): 120–180 μm ($n = 37$) long, 29–43 μm ($n = 35$) wide; tooth row 24% of total length; 7–8 ($n = 8$) large coarse medial teeth, the row terminates abruptly, proximal tooth largest, others uniform, their camber 45°, pitch 71°; 0–2 ($n = 8$) small basal teeth; 3–6 ($n = 8$) small lateral teeth.

Mandible (male) (Figs. 6F, 8F): 104–142 μm ($n = 19$) long, 20–32 μm ($n = 21$) wide; 2–6 ($n = 21$) medium medial teeth, 0–1 ($n = 21$) small lateral teeth.

Labrum (female) (Fig. 10F): 153–245 μm ($n = 14$) long, 19–39 μm ($n = 19$) wide; 21–32 ($n = 17$) long, slender, closely spaced spicules in single row on both ventrolateral and subapical surfaces. Spicules most abundant in this species of any examined.

Labrum (male) (Fig. 11F): 121–146 μm ($n = 8$) long, 19–44 μm ($n = 10$) wide; 14–36 ($n = 8$) long, slender, closely spaced spicules in 2–3 rows on the ventrolateral and subapical ventral surfaces. Spicules

most abundant in this species of any examined.

Hypopharynx (female) (Fig. 12F): 152–245 μm ($n = 15$) long, 4–37 μm ($n = 17$) wide; 0–9 ($n = 17$) long, slender spicules on the apex, absent from lateral margins.

Hypopharynx (male) (Fig. 13F): 120–156 μm ($n = 11$) long, 13–20 μm ($n = 10$) wide; 10–19 ($n = 9$) long, very slender spicules on pointed apex, absent from margins.

Palpal sensory organ (female) (Fig. 16F): 4–9 ($n = 15$) closely grouped sensilla 17–21 μm ($n = 6$) long, heads spatulate.

Palpal sensory organ (male) (Fig. 17F): 2–7 ($n = 6$) closely grouped sensilla 11–12 μm ($n = 4$) long, heads spatulate.

Palpomyia subaspera. Mandible (female) (Figs. 1G, 4A): 226–238 μm ($n = 2$) long, 40–47 μm ($n = 2$) wide; tooth row 28% of total length; 9–10 ($n = 2$) large coarse medial teeth, largest midlength of tooth row, their camber 58°, pitch 85°; 2–2 ($n = 2$) small basal teeth; 3–4 ($n = 2$) minute to small lateral teeth.

Mandible (male) (Figs. 6G, 9A): 118–140 μm ($n = 5$) long, 20–27 μm ($n = 6$) wide; 3–7 ($n = 7$) medium medial teeth, 0–2 ($n = 7$) small lateral teeth.

Labrum (female) (no Fig.): 266 μm ($n = 1$) long, 52 μm ($n = 1$) wide; 21 ($n = 1$) spicules.

Labrum (male) (Fig. 11G): 144–150 μm ($n = 4$) long, 25–27 μm ($n = 3$) wide; 16–20 μm ($n = 3$) spicules, long and slender and replace midapical structures of females, minute to short on ventrolateral surfaces.

Hypopharynx (female) (no Fig.): 251 μm ($n = 1$) long, 49 μm ($n = 1$) wide; 36 ($n = 1$) spicules.

Hypopharynx (male) (Fig. 13G): 145–156 μm ($n = 3$) long, 20–21 μm ($n = 3$) wide; 7–20 ($n = 2$) medium length slender spicules on rounded apex and distal margins.

Palpal sensory organ (female) (Fig. 16G): 10 ($n = 1$) closely grouped sensilla 22–30 μm ($n = 6$) long, heads spatulate.

Palpal sensory organ (male) (Fig. 17G):

2–7 ($n = 6$) closely grouped sensilla 20–23 μm ($n = 4$) long, heads same diameter as stalk.

Palpomyia cressoni. Mandible (female) (Figs. 1H, 4B): 181–192 μm ($n = 7$) long, 40–50 μm ($n = 10$) wide; tooth row 20% of total length; 6–9 ($n = 10$) medium coarse medial teeth, largest midlength of tooth row then rapidly diminishing in size proximally, their camber 46°, pitch 86°; 1–4 ($n = 10$) small, basal teeth; 2–7 ($n = 10$) minute lateral teeth.

Mandible (male): no specimens.

Labrum (female) (Fig. 10G): 207–234 μm ($n = 3$) long, 32–40 μm ($n = 4$) wide; 15–21 ($n = 3$) spicules which are minute and widely spaced in a single row.

Labrum (male): no specimens.

Hypopharynx (female) (Fig. 12G): 209–230 μm ($n = 3$) long, 29–48 μm ($n = 5$) wide; 29–48 ($n = 5$) short spicules on apex and lateral margins.

Hypopharynx (male): no specimens.

Palpal sensory organ (female) (Fig. 16H): 6–9 ($n = 7$) closely grouped sensilla 20–26 μm ($n = 6$) long, heads spatulate.

Palpal sensory organ (male): no specimens.

Palpomyia lineata. Mandible (female) (Figs. 2A, 4C): 120–239 μm ($n = 8$) long, 37–49 μm ($n = 9$) wide; tooth row 25% of total length; 7–11 ($n = 14$) large coarse medial teeth, uniform on distal three-fourths of row, then diminishing rapidly; 3–8 ($n = 14$) small basal teeth; 5–11 ($n = 14$) small lateral teeth.

Mandible (male) (Figs. 6H, 9B): 120–184 μm ($n = 12$) long, 21–31 μm ($n = 11$) wide; 3–10 ($n = 16$) large medial teeth, 0–2 ($n = 16$) minute lateral teeth.

Labrum (female) (Fig. 10H): 235–258 μm ($n = 3$) long, 33–40 μm ($n = 4$) wide; 18–23 ($n = 2$) short, widely spaced spicules on ventrolateral surfaces, closely spaced on subapical surface.

Labrum (male) (Fig. 11H): 140–186 μm ($n = 5$) long, 23–33 μm ($n = 9$) wide; 9–22 ($n = 6$) medium slender to coarse spic-

ules on ventrolateral and subapical ventral surfaces, absent from apex.

Hypopharynx (female) (Fig. 12H): 269 μm ($n = 1$) long, 33–47 μm ($n = 2$) wide; 24 ($n = 1$) short, closely set spicules on rounded apex and margins.

Hypopharynx (male) (Fig. 13H): 173–186 μm ($n = 5$) long, 21–36 μm ($n = 7$) wide; 8–17 ($n = 6$) long, slender spicules on semirounded apex and distal margins.

Palpal sensory organ (female) (Fig. 16I): 11 ($n = 1$) longitudinally widely spaced sensilla 25–32 μm ($n = 6$) long, heads fusiform.

Palpal sensory organ (male) (Fig. 17H): 3–5 μm ($n = 9$) longitudinally widely spaced sensilla 17–17 μm ($n = 3$) long, heads fusiform.

Palpomyia plebeia. Mandible (female) (Figs. 2B, 4D): 146–171 μm ($n = 19$) long, 27–33 μm ($n = 22$) wide; tooth row 21% of total length; 6–8 ($n = 21$) large coarse medial teeth, largest proximal, their camber 55°, pitch 91°; 2–5 ($n = 21$) small basal teeth; 3–6 ($n = 22$) small lateral teeth.

Mandible (male) (Figs. 7A, 9C): 110–126 μm ($n = 18$) long, 17–29 μm ($n = 18$) wide; 3–11 ($n = 18$) large medial teeth, some bifurcate; 0–2 ($n = 18$) minute lateral teeth.

Labrum (female) (Fig. 10I): 110–197 μm ($n = 8$) long, 23–32 μm ($n = 10$) wide; 20–30 ($n = 8$) medium length, closely spaced spicules.

Labrum (male) (Fig. 11I): 130–153 μm ($n = 7$) long, 12–27 μm ($n = 11$) wide; 15–23 ($n = 7$) spicules which are long and slender and replace the midapical structures of females, short and coarse on ventrolateral surfaces.

Hypopharynx (female) (Fig. 12I): 161–205 μm ($n = 9$) long, 20–29 μm ($n = 10$) wide; 13–23 ($n = 6$) minute to short spicules on rounded apex and margins.

Hypopharynx (male) (Fig. 13I): 130–148 μm ($n = 6$) long, 16–20 μm ($n = 10$) wide; 10–16 ($n = 10$) short, slender or very short blunt spicules on rounded apex, minute ones on margins.

Palpal sensory organ (female) (Fig. 16J): 6–12 ($n = 12$) longitudinally widely spaced sensilla, 14–18 μm ($n = 6$) long, heads spatulate.

Palpal sensory organ (male) (Fig. 17I): 3–7 μm ($n = 14$) longitudinally widely spaced sensilla 17–20 μm ($n = 4$) long, heads spatulate.

Palpomyia rufa. Mandibles (female) (Figs. 2C, 4E): 137–239 μm ($n = 34$) long, 32–50 μm ($n = 34$) wide; tooth row 21% of total length; 6–9 ($n = 41$) large coarse medial teeth, largest proximal, their camber 46°, pitch 90°; 0–7 ($n = 41$) small basal teeth; 0–7 ($n = 40$) minute lateral teeth.

Mandible (male) (Figs. 7B, 9D): 110–162 μm ($n = 15$) long, 16–27 μm ($n = 15$) wide; 2–7 ($n = 15$) large medial teeth, no lateral teeth.

Labrum (female) (Fig. 10J): 210–291 μm ($n = 12$) long, 27–57 μm ($n = 16$) wide; 12–20 ($n = 10$) minute, closely spaced spicules.

Labrum (male) (Fig. 11J): 142–180 μm ($n = 10$) long, 20–40 μm ($n = 10$) wide; 10–18 ($n = 8$) spicules, long and slender and replace the midapical structures of females, short and stout on subapical ventral surface, long and slender on ventrolateral surfaces.

Hypopharynx (female) (Fig. 12J): 189–310 μm ($n = 14$) long, 19–51 μm ($n = 16$) wide; 9–18 μm ($n = 6$) short spicules on rounded apex and margins.

Hypopharynx (male) (Fig. 13J): 142–192 μm ($n = 8$) long, 17–36 μm ($n = 9$) wide; 0–18 ($n = 8$) short spicules, blunt on apex, sharp and widely spaced on lateral margins.

Palpal sensory organ (female) (Fig. 16K): 1–12 ($n = 18$) longitudinally widely spaced sensilla, 16–19 μm ($n = 6$) long, heads spatulate.

Palpal sensory organ (male) (Fig. 17J): 2–5 ($n = 13$) longitudinally widely spaced sensilla 16–20 μm ($n = 5$) long, heads spatulate.

Palpomyia pseudorufa. Mandible (female) (Figs. 2D, 4F): 145–173 μm ($n = 28$) long, 23–33 μm ($n = 29$) wide; tooth row

23% of total length; 6–8 ($n = 35$) large coarse medial teeth, largest midlength of row, their camber 68°, pitch 72°; 0–4 ($n = 35$) small basal teeth; 0–5 ($n = 35$) minute lateral teeth.

Mandible (male) (Figs. 7C, 9E): 101–130 μm ($n = 22$) long, 16–24 μm ($n = 16$) wide; 4–6 μm ($n = 22$) large short medial teeth, no lateral teeth.

Labrum (female) (Fig. 10K): 170–210 μm ($n = 11$) long, 12–31 μm ($n = 14$) wide; 10–24 ($n = 9$) short closely spaced spicules.

Labrum (male) (Fig. 11K): 113–141 μm ($n = 8$) long, 13–20 μm ($n = 8$) wide; 7–17 ($n = 9$) spicules which are long and slender and replace the midapical structures of females, short and coarse on ventrolateral surfaces.

Hypopharynx (female) (Fig. 12K): 170–210 μm ($n = 12$) long, 15–25 μm ($n = 9$) wide; 11–26 ($n = 8$) medium, coarse, widely spaced spicules on flattened apex and margins.

Hypopharynx (male) (Fig. 13K): 118–140 μm ($n = 11$) long, 12–17 μm ($n = 9$) wide; 10–18 μm ($n = 11$) minute to short spicules on apex and margins.

Palpal sensory organ (female) (Fig. 16L): 3–6 ($n = 17$) longitudinally widely spaced sensilla 20–21 μm ($n = 5$) long, heads spatulate.

Palpal sensory organ (male) (Fig. 17K): 1–6 ($n = 17$) longitudinally spaced sensilla 17–21 μm ($n = 5$) long, heads spatulate.

Palpomyia basalis. Mandible (female) (Figs. 2E, 5A): 146–157 μm ($n = 4$) long, 33–37 μm ($n = 4$) wide; tooth row 19% of total length; 6–6 ($n = 8$) medium, coarse, widely spaced medial teeth, uniform size, their camber 38°, pitch 103°; 0–3 ($n = 8$) small basal teeth; 3–5 ($n = 8$) minute lateral teeth.

Mandible (male) (Figs. 7D): 102–108 μm ($n = 2$) long, 20–20 μm ($n = 2$) wide; no data on teeth.

Labrum (female) (Fig. 10L): 180–187 μm ($n = 2$) long, 16–40 μm ($n = 2$) wide;

no data on number of spicules which are short to minute.

Labrum (male) (Fig. 11L): 144 μm ($n = 1$) long, 16 μm ($n = 1$) wide; 16 ($n = 1$) short, slender spicules on ventrolateral and subapical ventral surfaces.

Hypopharynx (female) (Fig. 12L): 161–192 μm ($n = 2$) long, 13–15 μm ($n = 2$) wide; 6–8 ($n = 2$) long, slender spicules on apex, absent on margins.

Hypopharynx (male) (Fig. 13L): 141 μm ($n = 1$) long, 31 μm ($n = 1$) wide; 6–8 ($n = 2$) medium length, filiform spicules on pointed apex, absent on margins.

Palpal sensory organ (female): no specimens.

Palpal sensory organ (male): no specimens.

Palpomyia flaviceps. Mandible (female) (Figs. 2F, 5B): 125–172 μm ($n = 22$) long, 27–39 μm ($n = 24$) wide; tooth row 20% of total length; 4–9 ($n = 33$) medium coarse medial teeth, largest proximal, their camber 41°, pitch 78°; 0–3 ($n = 33$) small basal teeth; 0–5 ($n = 33$) small lateral teeth.

Mandible (male): no specimens measured.

Labrum (female) (Fig. 10M): 153–186 μm ($n = 7$) long, 24–64 μm ($n = 13$) wide; 9–29 ($n = 10$) short, closely spaced spicules on ventrolateral surfaces, sparse subapical ones.

Labrum (male): no specimens.

Hypopharynx (female) (Fig. 12M): 145–188 μm ($n = 12$) long, 13–28 μm ($n = 11$) wide; 0–10 ($n = 5$) long, filiform spicules on rounded apex, absent on margins.

Hypopharynx (male): no specimens.

Palpal sensory organ (female) (Fig. 16M): 2–8 ($n = 18$) longitudinally widely spaced sensilla 24–29 μm ($n = 5$) long, heads fusiform.

Palpal sensory organ (male): no specimens.

Palpomyia scalpellifera. Mandible (female) (Figs. 2G, 5C): 133–203 μm ($n = 8$) long, 28–44 μm ($n = 8$) wide; tooth row 15% of total length; 6–7 ($n = 8$) large coarse medial teeth, distal ones largest, di-

minishing slightly proximally, their camber 48°, pitch 90°; 1–3 ($n = 8$) small basal teeth; 3–7 ($n = 7$) small lateral teeth.

Mandible (male) (Figs. 7E, 9F): 100–132 μm ($n = 4$) long, 21–24 μm ($n = 4$) wide; 3–6 ($n = 4$) large medial teeth; no ($n = 4$) lateral teeth.

Labrum (female) (Fig. 10N): 162–217 μm ($n = 4$) long, 25–32 μm ($n = 4$) wide; no data on number of spicules which are medium and closely spaced on subventral surfaces, sparse subapical ones.

Labrum (male) (Fig. 11M): 133 μm ($n = 1$) long, 15 μm ($n = 1$) wide; 11 ($n = 1$) spicules, long and slender on tip, short and slender to stout on distal lateral and subapical ventral surfaces.

Hypopharynx (female) (Fig. 12N): 165–219 μm ($n = 3$) long, 20–28 μm ($n = 3$) wide; 9–11 ($n = 2$) long, slender spicules on rounded apex and distal margins.

Hypopharynx (male) (Fig. 13M): 132 μm ($n = 1$) long, 11–20 μm ($n = 2$) wide; 4 ($n = 1$) short to medium length spicules on pointed apex and distal margins.

Palpal sensory organ (female) (Fig. 16N): 6–14 ($n = 5$) longitudinally widely spaced sensilla 30–32 μm ($n = 5$) long, heads spatulate.

Palpal sensory organ (male) (Fig. 17L): 6–10 ($n = 2$) longitudinally widely spaced sensilla 17–19 μm ($n = 5$) long, heads spatulate.

Palpomyia hastata. Mandible (female) (Figs. 2H, 5D): 144–150 μm ($n = 2$) long, 32–34 μm ($n = 2$) wide; tooth row 17% of total length; 6–6 ($n = 2$) large coarse medial teeth, distal ones uniform size, proximal one largest, their camber 46°, pitch 97°; 1–2 ($n = 2$) small basal teeth; 0–3 ($n = 2$) small lateral teeth.

Mandible (male): no specimens.

Labrum (female) (Fig. 10O): no data on length, 29 μm ($n = 1$) wide; 18 ($n = 1$) medium, closely spaced spicules.

Labrum (male): no specimens.

Hypopharynx (female) (Fig. 12O): no data on length; 20 μm ($n = 1$) wide; 6 ($n = 1$) long slender spicules on rounded apex.

Hypopharynx (male): no specimens.

Palpal sensory organ (female) (Fig. 16O): 12 ($n = 1$) longitudinally widely spaced sensilla 18–24 ($n = 5$) long, heads spatulate.

Palpal sensory organ (male): no specimens.

DISCUSSION

Mandibles of female Palpomyiini resemble those of other entomophagous ceratopogonids, e.g. Ceratopogonini (McKeever et al. 1991), Heteromyiini and Sphaeromiini (personal observations) Stenoxenini (Wirth and Ratanaworabhan 1972) of the Ceratopogoninae, and ectoparasitic *Atrichopogon meloesugans* Kieffer and *A. lucorum* (Meigen) of the Forcipomyiinae (Glukhova 1981) in having large, widely-spaced retrorse teeth. Mandibles of the subgenus *Trithecoides* of *Culicoides* (Culicoidini), as illustrated by Glukhova for *C. humeralis* (1982), have large retrorse teeth that are similar in shape and approach the size of those of some Palpomyiini and Ceratopogonini.

A second characteristic common to Palpomyiini and many members of Ceratopogonini, Heteromyiini and Sphaeromiini is the presence of antrorse teeth on the lateral edge of their mandibles. Lateral antrorse mandibular teeth also occur in *Simulium venustum* Say (Nicholson 1945) and *Culicoides (Trithecoides) anophelis* Edwards (Glukhova 1982) in *C. (T.) flavescens* Macfie, and in *C. (T.) paraflavescens* Wirth and Hubert (Wirth and Hubert 1989). Their function in all of these groups is unknown, but they may assist with enlargement of the wound in the exoskeleton of prey. A third characteristic common to each of these four tribes is their reduced, unarmed laciniae, except for members of the *anophelis* group of *Trithecoides* that feed on mosquitoes and phlebotomine sand flies and that have strong teeth on the laciniae (Wirth and Hubert 1989).

Mandibles of Palpomyiini function in the same manner as reported for Ceratopogon-

ini (McKeever et al. 1991). The initial incision in the prey's integument is made by antrorse distal mandibular teeth and enlarged by sawing action of the antrorse teeth. Mandibular action during this process is the same as that for *Culicoides* as described by McKeever et al. (1988) and Sutcliffe and Deepan (1988), and for *Simulium* Latreille as described by Sutcliffe and McIver (1984). Other elements of the proboscis enter the wound made by the mandibles, but presence of antrorse spicules on the labrum and hypopharynx and absence of armature on the laciniae preclude these structures from functioning in producing the incision.

Once the proboscis is inserted, saliva containing a strong protease flows through the salivary canal of the hypopharynx and digests the prey (Downes 1971). The digested material is drawn from the prey through the food canal formed by the labrum dorsally, the mandibles ventrally and the laciniae laterally. Thus, the mandibles separate the food canal from the salivary canal.

Although all reports indicate that Palpomyiini usually feed on male Chironomidae and Ephemeroptera, Downes (1978) reported that his few records for *B. glabra* and *P. lineata* indicated that they select moderate to large prey species from these groups. This is the only specific reference to feeding by the species that we examined. During a two-week study at Loch Lomond, Scotland in 1960, Downes (1978) found that four species of *Palpomyia*, in the *flavipes* group as defined by Grogan and Wirth (1979), fed exclusively on mayflies, while a species of *Bezzia* and another species of *Palpomyia* fed only on chironomids.

Elements of the proboscis are basically similar in females of the 16 species examined, but species specific variations exist in the mandibles, labrum and hypopharynx. Grogan and Wirth (1975, 1979) separated the Nearctic species of *Palpomyia* into four species groups, viz., *tibialis*, *lineata*, *distincta*, and *flavipes*, on the basis of their

male and female genitalia. Mandibular teeth of the first three of these groups (Figs. 4A–F) are longer and larger than those of either the *flavipes* group, viz. *P. basalis*, *hastata*, *altispina*, and *flaviceps*, (Figs. 5A–D) or of species of *Bezzia* (Figs. 3A–E), with the exception of *B. glabra* which has longer teeth than those of *P. pseudorufa*. *Phaenobezzia opaca* has the longest teeth ($\bar{x} = 6.2 \mu\text{m}$, $n = 39$) of any species studied except those of *Palpomyia subaspera* ($\bar{x} = 8.0 \mu\text{m}$, $n = 2$). Basic similarities probably are interrelated with a common method of feeding, viz., sucking the saliva-digested contents of their prey, and their food specialization, i.e. males of their own species and males of Chironomidae and Ephemeroptera. Species specific differences in the various structures probably reflect minor differences in the restricted range of prey.

In contrast to minor differences exhibited by elements of the proboscis of Palpomyiini, Glukhova (1981) reported basic similarity with marked differences in all elements of the proboscis of species of *Atrichopogon*. She attributed the differences to the diversity in prey (Coleoptera, Neuroptera, and Lepidoptera) and to their feeding on different parts of the body (wing veins, thorax, and abdomen) of their prey.

Male Nematocera belonging to species in which the females are entomophagous and hematophagous have unarmed mandibles that are smaller and less sclerotized than those of females and are thought to be nectar feeders (Downes 1971). In a later paper, Downes (1978) described the behavior of *Bezzia* feeding on honeydew and expressed the opinion that such feeding would be found to be a normal activity of both sexes of all predaceous midges. Mandibles of male Palpomyiini are fairly typical of entomophagous Ceratopogoninae. They differ from those of some other entomophagous groups, e.g. Ceratopogonini (McKeever et al. 1991) in having large antrorse, pointed teeth on their medial edge. These teeth may be as large as the retrorse teeth of females,

but their shape precludes their functioning as biting structures.

The poorly sclerotized labrum of female Palpomyiini has antrorse spicules of various shapes, rather than teeth, and is therefore not adapted for active penetration of the prey. These spicules are most abundant in *P. opaca*. The labrum functions as the dorsal wall of the food canal and the sensilla basiconica on its ventral surface probably function as chemoreceptors that monitor incoming food. In *Tabanus nigrovittatus* Macquart, similarly located sensilla have four dendrites entering each sensillum and were considered to be chemosensory by Stoffolano and Yin (1983). The two terminal peg-like structures in species of Palpomyiini resemble the pair of peg-shaped sensilla immediately proximal to the terminal tricuspid teeth of *Culicoides* (McKeever et al. 1988). Sutcliffe (1994) states that a pair of "terminal labral pegs" is present in Culicidae, Simuliidae and Ceratopogonidae and that they are equipped with both chemosensory and mechanosensory elements. The peg-like structures in Palpomyiini probably are homologous to those in the foregoing three families and are chemoreceptors, mechanoreceptors or both.

The labra of females of other species of the family may be highly sclerotized and armored; e.g. four species of mammal-feeding *Culicoides* (McKeever et al. 1988) that have two tricuspid terminal teeth with a pair of sensilla at their base. The labra of species of *Forcipomyia* Meigen (Forcipomyiinae) are highly variable, with pointed apices with short lateral spicules in caterpillar feeders, smooth rounded apices in those that feed on Odonata, smooth apices reinforced by longitudinal sclerotized thickenings in those that feed on amphibia, and apices with long bristles (spicules) on the edges and short spicules on the dorsal surfaces in those that feed on hemolymph from wing veins of various insects (Glukhova 1981).

The labra of male Palpomyiini are shorter, narrower, less sclerotized, and have lon-

ger and fewer spicules than conspecific females. The terminal structures present in females are smaller and reduced in number or absent. A similar relationship has been reported for Ceratopogonini (McKeever et al. 1991) and for two species of frog-feeding *Corethrella* Coquillett (McKeever 1986). Male *P. opaca* have a significantly greater number of spicules than any other species examined. Labra of males are species specific, but differences among species are less pronounced than in labra of females.

The hypopharynx of females is unarmed; its edges are either smooth or bear antrorse spicules as reported for *Forcipomyia* (Glukhova 1981) and Ceratopogonini (McKeever et al. 1991). The shape and orientation of its spicules indicate that it has no function in penetrating the prey, but enters the incision made by the mandibles and conducts saliva into the wound through its salivary duct.

The hypopharynx of females exhibits some generic differences in its shape and specific differences in distribution of its spicules. The hypopharynx of *Phaenobezzia opaca* (Fig. 12F) differs from those of species of *Bezzia* (Figs. 12A–E) and *Palpomyia* (Figs. 12G–O) in being more pointed and from species of *Bezzia* in lacking lateral spicules; males also have a more pointed hypopharynx (Figs. 13F) than species of *Bezzia* (Figs. 13A–E) and *Palpomyia* (Figs. 13G–M). Females of the *flavipes* group of *Palpomyia* differ from those of other species of the genus in lacking lateral spicules (Figs. 12L–O), but do not differ appreciably from each other. Terminal spicules are filiform in species lacking lateral spicules.

The hypopharynx of males of all species has both terminal and lateral antrorse spicules; in most species they are larger than in conspecific females. The function of these spicules is unknown for either sex, and they are completely absent in some entomophagous *Forcipomyia* (Glukhova 1981).

The weakly sclerotized, unarmored laciniae of Palpomyiini, like those of Cerato-

pogonini (McKeever et al. 1991), serve only as lateral boundaries of the food canal of the proboscis. They differ from those of some species of entomophagous *Forcipomyia* which have strongly armored laciniae similar in degree of development to those of hematophagous *Culicoides* and are thought by Glukhova (1981) to serve in piercing the integument of and attachment to the flying prey.

Sensilla in the maxillary palp sensory organ differ among species with respect to their number, points of origin on the palp of the individual sensilla, shape of their head, and their total length; a combination of these characters makes the sensory organs species specific. Thus, in females of all species of *Bezzia* (Figs. 16A–E) and in *Phaenobezzia opaca*, *Palpomyia subaspera* and *P. cressoni* (Figs. 16F–H), the sensilla originate in close proximity to each other and the heads are in approximately the same plane with respect to the long axis of the palpal segment. In the other seven species of *Palpomyia* (Figs. 16I–O) the points of origin of the individual sensilla may extend over one-half the length of the palpal segment and proximal sensilla may not extend to the point of origin of distal ones. Sensilla of females vary in mean length from 11.2 μm ($n = 6$) in *B. glabra* to 37.5 μm ($n = 3$) in *B. imbifida*. Heads of sensilla of male and female *B. dorsasetula* (Figs. 17E, 16E) and *P. lineata* (Figs. 17H, 16I) are fusiform, heads of sensilla of male *P. subaspera* (Fig. 17G) are approximately the same diameter as the stalk and those of females and males of all other species are spatulate.

Palpal sensilla are reported to be olfactory receptors, including carbon dioxide detectors, in *Culicoides* (Rowley and Cornford 1972, Chu-Wang et al. 1975) and are thought to function as host detectors. However, present evidence indicates that female Palpomyiini rely on visual rather than olfactory stimuli when hunting and capturing their prey. *Bezzia* and *Palpomyia* are able to recognize visually distinctive areas that

serve as swarm markers for their prey, even though no prey is present, and hover there for long periods until prey individuals accumulate (Downes 1978). This indicates that in predaceous Ceratopogonidae the palpal sensilla serve little or no function in locating prey. Therefore, the number of sensilla should be approximately the same in both sexes of a given species and this was true for all species we examined. In contrast, some species of female *Culicoides*, which locate their hosts by olfactory stimuli, have four-fold increase in sensilla than do males of the same species (Rowley and Cornford 1972). For example, female *C. nubeculosus* Meigen have 12–17 sensilla per organ compared with 3–7 in males (Messaddeq et al. 1989). Their function in both sexes of Palpomyiini is unknown.

LITERATURE CITED

- Brinson, E. J., S. McKeever, and D. V. Hagan. 1993. Comparative study of mouthparts of the phlebotomine sand flies *Lutzomyia longipalpis*, *L. shannoni*, and *Phlebotomus papatasi* (Diptera: Psychodidae). *Annals of the Entomological Society of America* 86: 470–483.
- Chaika, S. Y. 1978. The fine structure of the chemoreceptors of the biting midges (Diptera: Ceratopogonidae). *Vestnik Moskovskogo Universiteta Seriya XVI Biologiya* 2: 21–28 (In Russian with English summary.)
- Chu-Wang, I., R. C. Axtell, and D. L. Kline. 1975. Antennal and palpal sensilla of the sand fly *Culicoides furens* (Poey) (Diptera: Ceratopogonidae). *International Journal of Insect Morphology and Embryology* 4: 131–149.
- Dow, M. I. and E. C. Turner, Jr. 1976. A taxonomic revision of the Nearctic species of the genus *Bezzia* (Diptera: Ceratopogonidae). *Virginia Polytechnic Institute and State University Research Division Bulletin* 103: 1–162.
- Downes, J. A. 1971. The ecology of blood-sucking Diptera: an evolutionary perspective, pp. 232–258. *In* Fallis, A. M., ed., *Ecology and physiology of parasites*. University of Toronto Press, Toronto, Canada.
- . 1977. Evolution of feeding habits in Ceratopogonidae. *Mosquito News* 37: 279–280.
- . 1978. Feeding and mating in the insectivorous Ceratopogonidae (Diptera). *Memoirs of the Entomological Society of Canada* 104: 1–62.
- Gad, A. M. 1951. The head capsule and mouth-parts in the Ceratopogonidae (Diptera-Nematocera). *Bulletin Societe Fouad I^{er} Entomologique* 35: 17–75.
- Glukhova, V. H. 1981. A comparative morphological review of the mouthparts of the females and males in the subfamilies Dasyheleinae and Forcipomyiinae. *Entomologicheskoe Obozrenie USSR* 60: 62–76 (in Russian; translation in *Entomological Review* 60: 59–72, 1981.)
- . 1982. On the structure of the mouthparts in bloodsucking midges of the subgenus *Trithecooides* of the genus *Culicoides* (Ceratopogonidae). *Parazitologiya* 16: 155–159 (In Russian with English summary.)
- Grogan, W. L., Jr. and W. W. Wirth. 1975. A revision of the genus *Palpomyia* Meigen of northeastern North America (Diptera: Ceratopogonidae). *University of Maryland Agricultural Experiment Station Miscellaneous Publication* 875, College Park. 49 pp.
- . 1979. The North American predaceous midges of the genus *Palpomyia* Meigen (Diptera: Ceratopogonidae). *Memoirs of the Entomological Society of Washington* 8: 1–125.
- . 1981. A new American genus of predaceous midges related to *Palpomyia* and *Bezzia* (Diptera: Ceratopogonidae). *Proceedings of the Biological Society of Washington* 94: 1279–1305.
- . 1988. The predaceous midges of the world (Diptera: Ceratopogonidae; tribe Ceratopogonini). *Flora and Fauna Handbook* 4. Brill, New York.
- Lewis, D. J. 1973. Phlebotomidae and Psychodidae (sand flies and moth flies), pp. 155–179. *In* Smith, K. G. V., ed., *Insects and other arthropods of medical importance*. British Museum (Natural History), London.
- McKeever, S. 1986. Mouthparts of the four North American *Corethrella* species (Diptera: Chaoboridae), with detailed study of *C. appendiculata*. *Journal of Medical Entomology* 23: 502–512.
- McKeever, S., D. V. Hagan, and W. L. Grogan, Jr. 1991. Comparative study of mouthparts of ten species of predaceous midges of the tribe Ceratopogonini (Diptera: Ceratopogonidae). *Annals of the Entomological Society of America* 84: 93–106.
- McKeever, S., M. D. Wright, and D. V. Hagan. 1988. Mouthparts of females of four *Culicoides* species (Diptera: Ceratopogonidae). *Annals of the Entomological Society of America* 81: 332–341.
- Messaddeq, M., M. Fabre, and M. Kremer. 1989. Scanning electron microscopy study of the sense organs in *Culicoides nubeculosus* (Diptera: Ceratopogonidae). *Annales de Parasitologie Humaine et Comparee* 64: 224–237.
- Nicholson, H. P. 1945. The morphology of the mouthparts of the non-biting blackfly, *Eusimulium dactotense* D. and S., as compared with those of the biting species, *Simulium venustum* Say (Diptera:

- Simuliidae). *Annals of the Entomological Society of America* 38: 281–297.
- Fowley, W. A. and M. Cornford. 1972. Scanning electron microscopy of the pit of the maxillary palp of selected species of *Culicoides*. *Canadian Journal of Zoology* 50: 1207–1210.
- Spinelli, G. R. and W. L. Grogan, Jr. 1985. *Clastriatomyia* a new Neotropical genus of predaceous midges related to *Palpomyia* and *Bezzia* (Diptera: Ceratopogonidae). *Proceedings of the Entomological Society of Washington* 87: 329–334.
- Stoffolano, J. G., Jr., and L. R. S. Yin. 1983. Comparative study of the mouthparts and associated sensilla of adult male and female *Tabanus nigrovittatus* (Diptera: Tabanidae). *Journal of Medical Entomology* 20: 11–32.
- Sutcliffe, J. F. 1994. Structure and possible functions of the labral tip complex in haematophagous members of Culicidae, Simuliidae and Ceratopogonidae, pp. 216–217. In J. E. O'Hara [ed.], *Third International Congress of Dipterology Abstract Volume*. Biological Resources Division CLBRR Agriculture Canada, Ottawa.
- Sutcliffe, J. F. and P. D. Deepan. 1988. Anatomy and function of the mouthparts of the biting midge *Culicoides sanguisuga* (Diptera: Ceratopogonidae). *Journal of Morphology* 198: 353–365.
- Sutcliffe, J. F. and S. B. McIver. 1984. Mechanics of blood-feeding in blackflies (Diptera: Simuliidae). *Journal of Morphology* 180: 125–144.
- Wirth, W. W. 1983a. A review of the American predaceous midges of the *Bezzia nobilis* group (Diptera: Ceratopogonidae). *Proceedings of the Entomological Society of Washington* 85: 670–685.
- . 1983b. The North American species of the *cockerelli* and *dorsasetula* groups of the predaceous midge genus *Bezzia*, subgenus *Homobezzia* (Diptera: Ceratopogonidae). *Proceedings of the Entomological Society of Washington* 85: 762–782.
- Wirth, W. W. and W. L. Grogan, Jr. 1982. The predaceous midges of the genus *Phaenobezzia* in North America (Diptera: Ceratopogonidae). *Memoirs of the Entomological Society of Washington* 10: 179–192.
- . 1983. The Nearctic species of the *Bezzia bivittata* group (Diptera: Ceratopogonidae). *Proceedings of the Biological Society of Washington* 96: 489–523.
- Wirth, W. W. and A. A. Hubert. 1959. *Trithecoides*, a new subgenus of *Culicoides* (Diptera: Ceratopogonidae). *Pacific Insects* 1: 1–38.
- . 1989. The *Culicoides* of Southeast Asia (Diptera: Ceratopogonidae). *Memoirs of the American Entomological Institute* 44: 1–508.
- Wirth, W. W. and N. C. Ratanaworabhan. 1972. A revision of the tribe Stenoxenini (Diptera: Ceratopogonidae). *Annals of the Entomological Society of America* 65: 1368–1388.